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Contents

Botany Volume 14

Page

No 1 Cytological observations on Indian subcontinent and Chinese *Dryopteris* and *Polystichum* (Pteridophyta: Dryopteridaceae)
M. Gibby 1

No 2 A redisposition of the species referred to the ascomycete genus *Microthelia*
D. L. Hawksworth 43

No 3 A classification of the genus *Dryopteris* (Pteridophyta: Dryopteridaceae)
C. R. Fraser-Jenkins 183

No 4 Evolutionary cladistics of marattialean ferns
C. R. Hill & J. M. Camus 219

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Cytological observations on Indian subcontinent and Chinese *Dryopteris* and *Polystichum* (Pteridophyta: Dryopteridaceae)

Mary Gibby

Botany series Vol 14 No 1 29 August 1985

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Cytological observations on Indian subcontinent and Chinese *Dryopteris* and *Polystichum* (Pteridophyta: Dryopteridaceae)

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Contents

Synopsis 1
Introduction 1
Materials and methods 1
Results and discussion 2
Dryopteris 2
Dryopteris hybrids 9
Polystichum 9
Other genera 12
Acknowledgements 13
References 13
Figures 15

Synopsis

Cytological observations are reported for *Dryopteris* and *Polystichum* species from the Indian subcontinent and China. Fifty-nine species and three hybrids have been investigated, and of these, 29 constitute new cytological records. Chromosome counts of six species and one hybrid from other genera are also given.

Introduction

The importance of cytological studies in taxonomic investigations of ferns was first demonstrated by Manton (1950), who described polyploidy, hybridization, and apomixis in Pteridophytes. Hybridization and polyploidy are of widespread occurrence in *Dryopteris* and *Polystichum*, and apomixis is found in some sections of these genera. *Dryopteris* and *Polystichum* both have a basic chromosome number of 41, and the great majority of the tetraploid species of these two genera that have been investigated are allopolyploids. Several papers have been published on cytological investigation of *Dryopteris* and *Polystichum* from the Indian subcontinent (e.g. Mehra, 1961; Mehra & Loyal, 1965; Mehra & Khullar, 1980) but reports are lacking for Chinese material. The taxonomy and morphology of the majority of the *Dryopteris* species included in this paper will be described by Fraser-Jenkins (in press); it is hoped that a paper dealing with the *Polystichum* species will be published by Fraser-Jenkins at a later date.

Materials and methods

Living plants were collected by C. R. Fraser-Jenkins during 1977–1980 and brought into cultivation at Chelsea Physic Garden, London, or Bicknacre, Essex (CRFJ and CPG numbers), and plants were grown from spores by T. Reichstein in Basel (TR numbers). Cytological investigations were made either on root tip mitosis, or meiosis in spore mother cells. For mitosis, actively growing root-tips (*c.* 1 cm long) were collected (preferably the finer roots, and only

Bull. Br. Mus. nat. Hist. (Bot.) **14** (1): 1–42
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those with white or pale yellow tips) and placed into a saturated solution of l-bromonaphthalene (*c.* 2 drops in 20 ml water) for four hours at 20°C, or for 12–14 hours at 4°C. The roots were then washed, and transferred to 3:1, absolute ethanol: glacial acetic acid, and stored at −18°C until required (at least for 24 hours). They were then placed in 1N HCl at 60°C for 15 or 20 minutes and stained either in Feulgen (Schiff's reagent) for 2 hours, and squashed in 45% acetic acid, or (usually) in acetocarmine because this improves the staining of the chromosomes. For meiosis, young sori were fixed in 3:1, absolute ethanol: glacial acetic acid, stored at −18°C (for at least 24 hours) and squashed in acetocarmine. Photographs were taken on a Zeiss photomicroscope using Ilford FP4 or Agfaortho film, using phase contrast or bright field with a tri-green filter, and printed at a magnification of ×1000; the scale on the figures represents 10 μm.

Results and discussion

For each species, every plant that has been investigated is cited with its locality and collecting date. Counts obtained from root tip mitosis are given as 2n numbers. Where meiosis has been investigated this is stated, together with the cytological analysis obtained. Reports by previous authors are given for each species, where applicable.

Dryopteris

1. *Dryopteris podophylla* (Hook.) Kuntze
   CRFJ 10069: 450 m, Victoria Peak, Hong Kong Island, (Brit.) China, 29 April 1980. 2n = 82 (Figs 1a, b). Diploid.

2. *Dryopteris scottii* (Beddome) Ching
   CRFJ 10293: 150 m Lopchu, nr Darjeeling, W. Bengal, India, 19 Oct. 1980. 2n = 164. Tetraploid.
   This confirms previous counts by Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965). Plants of *D. scottii* from Taiwan are reported as tetraploid by Kurita (1966), Mitui (1968), and Tsai & Shieh (1975); Hirabayashi (1970) reports it as a diploid apomict from Taiwan, based on a count of 82 bivalents at meiosis and the presence of both 32- and 64-spored sporangia. This may represent another taxon.

3. *Dryopteris hirtipes* subsp. *atrata* (Kunze) Fraser-Jenkins
   CRFJ 9169: 1650 m Kodaikanal, Palni hills, W. Ghats, Tamil Nadu, South India, 19 Dec. 1978. 2n = *c.*160.
   CRFJ 10376: 1800 m Lebong, Darjeeling, W. Bengal, India. 25 Oct. 1980. 2n = 164. Tetraploid.
   This is in agreement with earlier reports from India by Abraham, Ninan & Matthew (1962), Bhavanandan (1968), Bir & Vasudeva (1971), Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965). Manton & Sledge (1954) and Bhavanandan (1981) report a diploid sexual plant from Sri Lanka and S. India which is now separated as subsp. *hirtipes*.

4. *Dryopteris cycadina* (Franchet & P. A. L. Savat.) C. Chr.
   CRFJ 10491: ex hort. R.B.G. Kew; origin Japan, ex hort. *G. Downey*, Bicknacre, Essex, 18 July 1981. 2n = 123 (Figs 2a, b). Triploid apomict.
   The plant investigated here probably corresponds to that investigated by Manton (1950), who reports 2n = *c.*120 at mitosis and 123 bivalents in an 8-celled sporangium. In 16-celled sporangia she reports irregular meiosis composed largely of univalents. Mitui (1965) and Hirabayashi (1974) report this species as triploid from Japan.

5. *Dryopteris darjeelingensis* Fraser-Jenkins [In press]
   CRFJ 8559: 2200 m Manebhanjang to Sukia Pokhri, nr Darjeeling, W. Bengal, N. India, 16 Nov. 1978. 2n = 123; meiosis, 15–18 bivalents, 93–87 univalents in 16-celled sporangia (Figs 3a, b; 4a, b). Triploid apomict.

This is almost certainly the same species as that reported from the E. Himalaya (sub *D. atrata*) by Loyal (*in* Mehra, 1961); however Mehra & Loyal (1965) report equal numbers of bivalents and univalents at meiosis in 16-celled sporangia in their material.

6. *Dryopteris stenolepis* (Baker) C. Chr.
CRFJ 8820: 1800 m Khasi Hills, Shillong, Meghalaya, Assam, N. India, 24 Nov. 1978. 2n = 82 (Figs 5a, b); meiosis 82 bivalents (Figs 6a, b).
T. Reichstein 5066: as *CRFJ* 8820. Meiosis, 82 bivalents.
CRFJ 9933: 950 m Wu-Shien-Kang, Omei Shan, Szechuan, China, 11 April 1980. 2n = 82 (Figs 7a, b). Diploid apomict.

7. *Dryopteris dickinsii* (Franchet & P. A. L. Savat.) C.Chr.
CRFJ 9869: 1800 m Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82 (Figs 8a, b).
CRFJ 9876: as *CRFJ* 9869. 2n = *c.*82.
CRFJ 9966: 1500 m, as *CRFJ* 9869. 2n = 82.
CRFJ 9968: 1500 m, as *CRFJ* 9869. 2n = 82 (Figs 9a, b).
CRFJ 9969: 1500 m, as *CRFJ* 9869. 2n = 82 (Figs 10a, b).
CRFJ 10283: 2400 m Chhachpur, nr Jubbal, nr Simla, Himachal Pradesh, NW. India. Coll. *CRFJ, S. P. Khullar & J. B. S. Oberoi*, 22 Sept. 1980. 2n = *c.*80. Diploid.
This species is reported as diploid apomict from Japan by Kurita (1965) and Hirabayashi (1969, 1974).

8. *Dryopteris rosthornii* (Diels) C. Chr.
CRFJ 9926: 1700 m Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82 (Figs 11a, b). Diploid.
This species is reported as diploid apomict (? facultative, almost certainly in error) by Wang & Zhang (1981), sub *D. julaodongensis* nom. nud., from the same locality.

9. *Dryopteris neorosthornii* Ching
CRFJ 10304: 3600 m Sandakphoo Mt, Singalilla ridge, nr Darjeeling, W. Bengal, India, 21 Oct. 1980. 2n = 123.
CRFJ 10305: as *CRFJ* 10304. 2n = *c.*120. Triploid apomict.

10. *Dryopteris redactopinnata* Panigr. & S. K. Basu
CRFJ 7591: 3000 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, N. India, 26 Aug. 1978. 2n = 82. Diploid.

11. *Dryopteris yigongensis* Ching
CRFJ 6762: 2200 m Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Sept. 1977. 2n = *c.*120.
CRFJ 7612: 3000 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, N. India, 26 Aug. 1978. 2n = *c.*123 (Figs 12a, b).
CRFJ 7647: as *CRFJ* 7612. 2n = 123 (Figs 13a, b).
CRFJ 7657: as *CRFJ* 7612. 2n = 123 (Figs 14a, b).
CRFJ 10232: 2250 m Chhachpur, nr Jubbal, nr Simla, Himachal Pradesh, NW. India, coll. *CRFJ, S. P. Khullar & J. B. S. Oberoi*, 23 Sept. 1980. 2n = 123. Triploid apomict.

12. *Dryopteris acuto-dentata* Ching
CRFJ 10481: 3600 m Sandakphoo Mt, Singalilla ridge, nr Darjeeling, W. Bengal, India, 21 Oct. 1980. ex hort. *G. Downey*, Bicknacre, Essex, 18 July 1981. 2n = 123.
CRFJ 10483B: as *CRFJ* 10481. 2n = 123. Triploid apomict.
This species is reported as a triploid apomict (sub *D. serrato-dentata*) from the E. Himalaya by Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965).

13. *Dryopteris lepidopoda* Hayata
CRFJ 9881: 1900 m Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82; meiosis, 82 bivalents (Figs 15a, b).
CRFJ 9923: 1700 m, as *CRFJ* 9881. 2n = *c*.82.
CRFJ 9927: 1700 m, as *CRFJ* 9881. 2n = 82. (Figs 16a, b).
CRFJ 10020: 2100 m below Chung-Chu-Sze temple, N. Zhi Shan, Kunming, Yunnan, China, 17 April 1980. 2n = 82.
T. Reichstein 4405: grown from spores ex *H. S. Puri* 20.4, 3000 m Kewsey, Lachung, N. Sikkim, India. 2n = 82.
T. Reichstein 4406: grown from spores ex *H. S. Puri* 20.16, N. Sikkim, India. 2n = 82. Diploid apomict.

14. *Dryopteris wallichiana* (Sprengel) N. Hylander
CRFJ 9880: 1900 m Yu Shien Sze temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82.
CRFJ 10364: 3000 m between Kalpokhri and Gairibas, Singalilla ridge, nr Darjeeling, W. Bengal, India, 22 Oct. 1980. 2n = *c*.82.
T. Reichstein 4082, grown from spores ex Taiwan, 2300 m Mt Ari-san, Kagi pref., 31 July 1976, leg. *Takumi Shiraiwa* 5437. 2n = 82. Diploid.
This species is reported as diploid apomict from the E. Himalaya by Loyal (1960) and Mehra & Loyal (1965), from Taiwan by Hirabayashi (1970), and has been found to be diploid from Peru (*M. Gibby & J. A. Barrett* 230, 4000 m Cordillera Blanca, Quebrada Honda, Vinoupampa, S. side, 19 July 1979), Costa Rica (3000 m, Chirripó National Park, Feb. 1983; ex hort. Chelsea Physic Garden, no. 4537), and from Sabah, Borneo (*A. C. Jermy* 15145:6, 3000 m Pakka Cave, Kinabalu National Park, Dec. 1980; ex hort. Chelsea Physic Garden no. 3575). *D. wallichiana* is reported as triploid apomict from Mexico by Mickel, Wagner & Chen (1966). Reports of triploids from S. India and Sri Lanka refer to *D. madrasensis*; a triploid reported from Nepal by Roy, Sinha & Sakya (1971) refers to *D. juxtaposita*. Triploids from New Guinea, collected by *B. Parris* (September 1980; ex hort. Chelsea Physic Garden nos. 3396–7) are referable to *D. parrisiae* Fraser-Jenkins (Figs 17a, b). Walker (1973) reports *D. wallichiana* as a tetraploid from Jamaica; this needs further investigation. It is known to be triploid in Zimbabwe.

15. *Dryopteris madrasensis* Fraser-Jenkins [In press]
CRFJ 9205: 1200 m Pillar Rocks, Kodaikanal, Palni Hills, W. Ghats, Tamil Nadu, S. India, 20 Dec. 1978. 2n = 123 (Figs 18a, b) Triploid apomict.
This is reported as triploid apomict (sub *D. wallichiana* or *D. paleacea*) from Sri Lanka (Manton & Sledge, 1954) and S. India (Bhavanandan, 1968, 1981).

16. *Dryopteris khullarii* Fraser-Jenkins [In press]
CRFJ 7226: 2450 m Jangal Chatti, Kedarnath Mt, Chamoli, Uttar Pradesh, N. India, 15 Oct. 1977. 2n = 123.
CRFJ 7227: as *CRFJ* 7226. 2n = *c*.123. Triploid apomict.

17. *Dryopteris sledgei* Fraser-Jenkins [In press]
CRFJ 9349: 2450 m Ootacamund, Dodabetta Mt, Nilgiri Hills, W. Ghats, Tamil Nadu, S. India, 26 Dec. 1978. 2n = 164.
CRFJ 9351: as *CRFJ* 9349. 2n = 164 (Figs 19a, b). Tetraploid.

18. *Dryopteris woodsiisora* Hayata
CRFJ 10400: 1600 m Between Ghoom and Kurseong, nr Darjeeling, W. Bengal, India, 26 Oct. 1980. 2n = *c*.82.
CRFJ 10401: as *CRFJ* 10400. 2n = 82. Diploid.

19. *Dryopteris chrysocoma* (Christ) C.Chr.
CRFJ 6773: 2200 m Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Aug. 1977. 2n = 82 (Figs 20a, b). Diploid.
This is in agreement with earlier reports by Verma & Loyal (1960), Loyal (*in* Mehra, 1961), Mehra & Loyal (1965), and Mehra & Khullar (1980).

20. *Dryopteris himachalensis* Fraser-Jenkins [In press]
T. Reichstein 4568: grown from spores, ex *CRFJ* 6879: 2700 m Kothi, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Sept. 1977. 2n = 123. Triploid.
D. himachalensis appears to be partially apomictic; most of the spores of the holotype are abortive with rather few spores that appear fertile. The paratype (obtained from the same population as the holotype) on which the chromosome count was made has a higher frequency of good spores than the holotype, and this matches specimens from SW. China.

21. *Dryopteris filix-mas* (L.) Schott
T. Reichstein 4548: grown from spores ex *CRFJ* 6364: 3000 m Lake Saif-ul-Malluk, Naran, Upper Kunhar (Kagan) valley, Hazara, N. Pakistan. 2n = *c.*164. Tetraploid.
This is the first report of the cytology of *D. filix-mas* from the Indian subcontinent. It has been reported widely from Europe (e.g. Manton, 1950) and N. America (e.g. Wagner & Hagenah, 1962) as a sexual tetraploid.

22. *Dryopteris serrato-dentata* (Beddome) Hayata
CRFJ 10480: 3600 m Sandakphoo Mt, Singalilla ridge, nr Darjeeling, W. Bengal, India, 21 Oct. 1980. 2n = *c.*160.
CRFJ 10489: as *CRFJ* 10480. 2n = 164. Tetraploid.
Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965) report this species as a sexual tetraploid from the E. Himalaya, along with a diploid sexual taxon which needs further investigation.

23. *Dryopteris barbigera* (T. Moore ex Hook.) Kuntze subsp. *barbigera*
T. Reichstein 4554: grown from spores ex. *CRFJ* 6487: 3200 m Mt Apharwat, Khilanmarg, nr Gulmarg, Pir Panjal range, nr Srinagar, Kashmir, NW. India, 24 Aug. 1977. 2n = 82. Diploid.
This agrees with earlier reports from the E. Himalaya by Loyal (*in* Mehra, 1961), Mehra & Loyal (1965), and Loyal (*in* Mehra & Khullar, 1980).

24. *Dryopteris blanfordii* (C. Hope) C.Chr. subsp. *blanfordii*
T. Reichstein 4552: grown from spores ex *CRFJ* 6479: 2600 m Mt Apharwat, Khilanmarg, Gulmarg, Pir Panjal Range, nr Srinagar, Kashmir, NW. India, 24 Aug. 1977. 2n = 123.
CRFJ 6810: 2700 m Kothi, Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Sept. 1977. 2n = 123 (Figs 21a, b).
CRFJ 7403: 2400 m Sind valley, Gund, Sonamarg to Ganderbal, nr Srinagar, Kashmir, N. India, 15 Aug. 1978. 2n = *c.*123.
CRFJ 7404: as *CRFJ* 7403. 2n = 123 (Figs 22a, b). Triploid apomict. This species is reported as a triploid apomict from the W. Himalaya by Mehra & Khullar (*in* Löve, 1970) and Mehra & Khullar (1980).

25. *Dryopteris sublacera* Christ
CRFJ 7596: 3000 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, N. India, 26 Aug. 1978. 2n = 123 (Figs 23a, b).
CRFJ 7601: as *CRFJ* 7596. 2n = *c.*120.
CRFJ 9978: 2250 m Tai-Hwa-Sze, Zhi Shan, Kunming, Yunnan, China, 17 April 1980. 2n = *c.*121.
CRFJ 9988: as *CRFJ* 9978. 2n = 123 (Figs 24a, b).
CRFJ 9989: as *CRFJ* 9978. 2n = *c.*121.

CRFJ 9992: as *CRFJ* 9978. 2n = 123.
CRFJ 9993: as *CRFJ* 9978. 2n = *c.*123.
CRFJ 9995: as *CRFJ* 9978. 2n = 123.
CRFJ 10006: as *CRFJ* 9978. 2n = *c.*122.
CRFJ 10022: 2100 m Chung-Chu-Sze, N. Zhi Shan, Kunming, Yunnan, China, 17 April 1980. 2n = *c.*121. Triploid apomict.

26. *Dryopteris odontoloma* (Beddome) C.Chr.
CRFJ 9318: 220 m Lovedale road, Ootacamund, Nilgiri Hills, W. Ghats, Tamil Nadu, S. India, 25 Dec. 1978. 2n = 123; meiosis, 8-celled sporangia, 123 bivalents; 16-celled sporangia, 18 bivalents and 87 univalents (Figs 25a, b), 13 bivalents and 97 univalents (Figs 26a, b). Triploid apomict.

27. *Dryopteris juxtaposita* Christ
CRFJ 6988: 2600 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = *c.*122.
CRFJ 6991: as *CRFJ* 6988. 2n = *c.*121.
CRFJ 6995: as *CRFJ* 6988. 2n = 123 (Figs 27a, b).
CRFJ 7161: 1350 m Narainkoti, Mandakini valley, nr Okimath, Chamoli, Uttar Pradesh, N. India, 14 Sept. 1977. 2n = *c.*120.
CRFJ 7163: as *CRFJ* 7161. Meiosis, 8-celled sporangia, 123 bivalents (Figs 29a, b); 16-celled sporangia, 41 bivalents + 41 univalents (Figs 30a, b).
CRFJ 7165: as *CRFJ* 7161. 2n = 123.
CRFJ 7184: as *CRFJ* 7161. Meiosis, 123 bivalents.
CRFJ 7241: 1700 m Joshimath, nr Rishikesh, Alaknanda valley, Chamoli, Uttar Pradesh, N. India, 17 Sept. 1977. 2n = 123. (Figs 28a, b).
T. Reichstein 4590: ex spores *CRFJ* 7241 above. Meiosis, 8-celled sporangia, 123 bivalents (Figs 31a, b); 16-celled sporangia, 8 trivalents + 33 bivalents + 33 univalents (Figs 32a, b).
CRFJ 7608: 3000 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, N. India, 26 Aug. 1978. 2n = 123.
CRFJ 7620: as *CRFJ* 7608. 2n = *c.*122.
CRFJ 8234: 1900 m Trijugi Naryan, Mandakini valley, nr Rudraprayag, Chamoli, Uttar Pradesh, N. India, 24 Oct. 1978. 2n = *c.*120.
CRFJ 9894: 1700 m Between Chao-Lao-Dung and Yu-Shien-Sze, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. Meiosis, 8-celled sporangia, 123 bivalents; 16-celled sporangia, *c.*123 univalents (Figs 33a, b). Triploid apomict.
Previous reports (sub *D. odontoloma*) are by Loyal (*in* Mehra, 1961), Mehra & Loyal (1965), and (sub *D. paleacea*) Roy, Sinha & Sakya (1971). Mehra & Loyal (1965) report *c.*14 trivalents, 27 bivalents, and 27 univalents in 16-celled sporangia of plants from Darjeeling.

28. *Dryopteris nigropaleacea* (Fraser-Jenkins) Fraser-Jenkins
CRFJ 6925: 2450 m Narkanda road, E. of Simla, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 82 (Figs 34a, b).
CRFJ 6927: as *CRFJ* 6925. 2n = 82.
CRFJ 6933: as *CRFJ* 6925. Meiosis, 41 bivalents (Figs 35a, b).
CRFJ 6936: as *CRFJ* 6925. 2n = *c.*80.
CRFJ 6939: as *CRFJ* 6925, Meiosis, 41 bivalents.
CRFJ 6940: as *CRFJ* 6925. Meiosis, 41 bivalents.
CRFJ 6990: 2600 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 82 (Figs 36a, b).
CRFJ 9840: Changla Gali, Murree Hills, nr Rawalpindi, Pakistan, Jan. 1979. 2n = 82.
T. Reichstein 4201: grown from spores ex *H. S. Puri* 615: Landigash, Simla, NW. India. 2n = 82. Sexual diploid.

Previous counts (sub *D. odontoloma*) are by Verma & Loyal (1960), Loyal (*in* Mehra, 1961), Mehra & Loyal (1965), Mehra & Khullar (1980).

29. *Dryopteris stewartii* Fraser-Jenkins
CRFJ 6332: 3000 m Giltidas, Babusar Pass, Upper Kunhar (Kagan) valley, Hazara, Pakistan, 9 Aug. 1977. 2n = 123 (Figs 37a, b).
CRFJ 6803: 2700 m Kothi, nr Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Sept. 1977. 2n = 123.
CRFJ 6804: as *CRFJ* 6803. 2n = *c.*123; meiosis 123 bivalents (Figs 38a, b).
CRFJ 6970: 2400 m Matiana, nr Simla, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 123 (Figs 39a, b).
CRFJ 7378: 2400 m Changla Gali, Ayubia, Murree Hills, Hazara, Pakistan, 6 Aug. 1978. 2n = 123.
CRFJ 9841: as *CRFJ* 7378. January 1979. 2n = 123. Triploid apomict.
Previous reports are by Gibby (*in* Fraser-Jenkins, 1978) and Mehra & Khullar (1980).

30. *Dryopteris fructuosa* (Christ) C.Chr.
CRFJ 9974: 2250 m Tai-Hwa-Sze temple, Zhi Shan, Kunming, Yunnan, China, 17 April 1980. 2n = *c.*121.
CRFJ 9996: as *CRFJ* 9974. 2n = 123 (Figs 40a, b).
CRFJ 10004: as *CRFJ* 9974. 2n = *c.*120. Triploid apomict.
Previous reports from the E. Himalaya are by Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965).

31. *Dryopteris basisora* Christ
CRFJ 9986: 2250 m Tai-Hwa-Sze temple, Zhi Shan, W. of Kunming, Yunnan, China, 17 April 1980. 2n = 123 (Figs 41a, b; 42a, b).
CRFJ 9990: as *CRFJ* 9986. 2n = 123. Triploid apomict.

32. *Dryopteris pteridiiformis* Christ
CRFJ 10028: 2100 m Chung-Chu-Sze, N. Zhi Shan, Kunming, Yunnan, China, 17 April 1980. 2n = 164 (Figs 43a, b). Tetraploid.

33. *Dryopteris subimpressa* Loyal
CRFJ 7217: Jangal Chatti, Kedarnath Mt, Chamoli, Uttar Pradesh, N. India, 15 Sept. 1977. 2n = *c.*82 (Figs 44a, b). Diploid.

34. *Dryopteris marginata* (Wallich ex C. B. Clarke) Christ
CRFJ 8974: 1800 m N. of Sohrarin, W. of Umtyngar, N. of Cherrapunji, S. of Shillong, Meghalaya St, Assam, India, 1 Dec. 1978, Meiosis, 41 bivalents. Sexual diploid.
This is reported as a sexual diploid from the E. Himalaya by Loyal (*in* Mehra, 1961) and Mehra & Loyal (1965).

35. *Dryopteris caroli-hopei* Fraser-Jenkins [In press]
CRFJ 6687: 1200 m Aiju, Joginder Nagar, nr Mandi, Himachal Pradesh, NW. India, 1 Sept. 1977. 2n = 82.
CRFJ 7045: 1900 m Simla, Himachal Pradesh, NW. India, 9 Sept. 1977. Meiosis 41 bivalents.
CRFJ 7055: as *CRFJ* 7045. 2n = 82.
CRFJ 7057: as *CRFJ* 7045. 2n = 82.
CRFJ 7058: as *CRFJ* 7045. 2n = *c.*82.
CRFJ 7062: as *CRFJ* 7045. 2n = 82 (Figs 45a, b).
CRFJ 7159: 1350 m Narainkoti, Mandakini valley, nr Okimath, Chamoli, Uttar Pradesh, N. India, 14 Sept. 1977. 2n = 82 (Figs 46a, b). Sexual diploid.

Previous counts (sub *D. marginata*) are by Verma & Loyal (1960), Loyal (*in* Mehra, 1961), Mehra & Loyal (1965), Mehra & Khullar (1980).

36. *Dryopteris porosa* Ching
CRFJ 9884: 1900 m Yu-Shien-Sze temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82.
CRFJ 9885: as *CRFJ* 9884. 2n = *c.*80.
CRFJ 9886: as *CRFJ* 9884. 2n = 82.
CRFJ 9887: as *CRFJ* 9884. 2n = *c.*82 (Figs 47a, b).
CRFJ 9890: as *CRFJ* 9884. 2n = 82.
CRFJ 9891: as *CRFJ* 9884. 2n = 82. Diploid.

37. *Dryopteris subtriangularis* (C. Hope) C.Chr.
CRFJ 9897: 1900 m Yu-Shien-Sze temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. Meiosis, 123 bivalents (Figs 48a, b). Triploid apomict.

38. *Dryopteris gymnosora* (Makino) C. Chr.
CRFJ 9939: 950 m Wu-Shien-Kang, Mt of 1000 temples, Omei Shan, Szechuan, China, 11 April 1980. 2n = 123 (Figs 49a, b). Triploid apomict.
Japanese plants of *D. gymnosora* are reported as triploid apomict by Kurita (1962; 1967), Hirabayashi (1967; 1974), and Mitui (1968).

39. *Dryopteris integriloba* C.Chr.
CRFJ 10065: 250 m Ding-Hu Shan Arboretum, Kao Yao, W. of Canton, Kwangtung, China, 24 April 1980. 2n = *c.*120 (Figs 50a, b).
CRFJ 10067: as *CRFJ* 10065. 2n = *c.*123 (Figs 51a, b). Triploid apomict.

40. *Dryopteris championii* (Benth.) C.Chr.
CRFJ 10056: 250 m Ding-Hu Shan Arboretum, Kao Yao, W. of Canton, Kwangtung, China, 24 April 1980. 2n = 82 (Figs 52a, b). Diploid.
Kurita (1966) reports this species as triploid from Japan; Hirabayashi (1967) reports both 123 and 82 bivalents at meiosis from one individual plant of *D. championii* from Japan; this phenomenon he also reports in other apomictic *Dryopteris* species, namely *D. erythrosora, D. hondoensis, D. fuscipes, D. decipiens,* and *D. nipponensis*. However, these findings probably result from mis-interpretation of meiosis in 16-celled sporangia of these species. For example, Plates 9a & 6 (p. 77) of Hirabayashi (1974) purport to show respectively triploid and diploid phases of *D. decipiens*; similarly 9c and d show diploid and triploid phases of *D. fuscipes*. In both cases the 'triploid phase' shows metaphase 1 in an 8-celled sporangium, with *c.*123 bivalents; the 'diploid phase' actually shows metaphase 1 in a 16-celled sporangium, and although 82 'bodies' are seen in the preparations, these consist of *c.*41 bivalents and *c.*41 univalents – the univalents being the small rod shaped bodies in the photographs. The presence of univalents is overlooked by Hirabayashi (1974) in 16-celled sporangia of other species, where this phenomenon is described.

41. *Dryopteris varia* (L.) Kuntze
CRFJ 10054: 250 m Ding-Hu Shan Arboretum, Kao Yao, W. of Canton, Kwangtung, China, 24 April 1980. 2n = 123 (Figs 53a, b).
CRFJ 10855: Victoria Peak, Hong Kong, (Brit.) China, 29 April 1980. 2n = 123. Triploid apomict.
Japanese plants of *D. varia* are reported as diploid apomict by Hirabayashi (1966, 1967, 1974) and as triploid apomict by Mitui (*in* Fabbri, 1965; Mitui 1966, 1968) and Hirabayashi (1970).

42. *Dryopteris viridescens* (Baker) Kuntze
CRFJ 9934: 950 m Wu-Shien-Kang, Mt of 1000 temples, Omei Shan, Szechuan, China, 11 April 1980. 2n = *c.*164. (Figs 54a, b).
CRFJ 10068: 450 m Victoria Peak, Hong Kong Island, (Brit.) China, 29 April 1980. 2n = 164 (Figs 55a, b). Tetraploid.

Dryopteris hybrids

43. *Dryopteris* × *flemingii* Fraser-Jenkins [In press]
(= *D. chrysocoma* × *D. juxtaposita*)
CRFJ 6968: 2400 m Matiana, between Simla and Narkanda, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 164 (Figs 56a, b). Tetraploid.
One parent, *D. juxtaposita*, is a triploid apomict, and it is possible that this hybrid is partially apomictic. The spores are largely abortive, but there are a few big spores that may be fertile.

44. *Dryopteris* × *wechteriana* Fraser-Jenkins [In press]
(= *D. chrysocoma* × *D. nigropaleacea)*
CRFJ 6948: 2450 m E. of Simla on Narkanda road, Himachal Pradesh, N. India, 6 Sept. 1977. 2n = 82; meiosis, mostly univalents (Figs 57a, b; 58a, b; 59a, b). Diploid.

45. *Dryopteris* × *zygo-parentalis* Fraser-Jenkins [In press]
(= *D. darjeelingensis* × *D. scottii*)
CRFJ 8577: 2200 m between Manebhanjang and Sukia Pokhri, nr Darjeeling, W. Bengal, N. India, 16 Nov. 1978. 2n = *c.*200 (Figs 60a, b). Pentaploid.
One putative parent, *D. darjeelingensis*, is a triploid apomict, and the hybrid *D.* × *zygo-parentalis* may be partially apomictic.

Polystichum

46. *Polystichum mehrae* Fraser-Jenkins & Khullar (in prep.)
CRFJ 6757: 2200 m above Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Aug. 1977. 2n = *c.*160.
CRFJ 6760: as *CRFJ* 6757. 2n = 164. Tetraploid.
NOTE BY C. R. FRASER-JENKINS: A tetraploid count for this species has been reported earlier by Mehra & Khullar (in Löve, 1970) and Khullar & Gupta (1978) under the name *P. acanthophyllum*; this name has been widely misapplied to the Himalayan plant, but the holotype of *P. acanthophyllum* (Franchet) Christ in Paris (P!) represents the same species as *P. horridipinnum* Hayata, and has straight fronds with overlapping pinnae, the segments bearing many, markedly long, aristate teeth. *P. acanthophyllum* is not present in the Indian subcontinent, and *P. mehrae* is uncommon in China, occurring in Yunnan, Szechuan, and SE. Tibet.

47. *Polystichum acutidens* Christ
CRFJ 9945: 1000 m between Wu-Shien-Kang and Hong-Chun-Ping temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 11 April 1980. 2n = 164 (Figs 61a, b).
CRFJ 9947: as *CRFJ* 9945. 2n = 164. (Figs 62a, b). Tetraploid.
NOTE BY C. R. FRASER-JENKINS: Previously known as *P. auriculatum* sensu auct. NE. India, but the Himalayan and SW. Chinese material does not represent the S. Indian species, now correctly known as *P. harpophyllum* (Zenk. ex Kunze) Sledge instead of *P. auriculatum* (L.) Presl.

48. *Polystichum discretum* (D. Don) J. Smith
CRFJ 6688: 900 m E. of Mandi, Beas river gorge, Simla, Himachal Pradesh, NW. India, 1 Sept. 1977. Meiosis, 41 bivalents.
CRFJ 6689: as *CRFJ* 6688. 2n = 82 (Figs 63a, b).
CRFJ 6695: as *CRFJ* 6688. Meiosis, 41 bivalents.
CRFJ 6697: as *CRFJ* 6688. Meiosis, 41 bivalents. Sexual diploid.
NOTE BY C. R. FRASER-JENKINS: Previously reported by Khullar & Gupta (1978), sub *P. indicum* Khullar & Gupta nom. nud., as a sexual diploid. The nomenclature of this species is complicated because the name *P. discretum* has been misapplied to *P. longipaleatum* Christ (= *P. setosum* auct.) and the name *P. nigropaleacum* (Christ) Diels, a synonym of *P. discretum*, has been misapplied to the common Himalayan member of the *P. makinoi* (Tagawa) Tagawa and *P. yunnanense* Christ aggregate, both due to lack of typification. The present species has recently been redescribed several times mainly by Indian and Japanese botanists as *P. kathmanduense* Nakaike, *P. wallichianum* Presl, and *P. indicum* Khullar & Gupta nom. nud.

49. *Polystichum piceo-paleaceum* Tagawa
CRFJ 6950: 2450 m Narkanda road, E. of Simla., Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 164.
CRFJ 7179: 1500 m N. of Phatta, Mandakini valley, N. of Rishikesh, Chamoli, Uttar Pradesh, N. India, 15 Sept. 1977. 2n = 164 (Figs 64a, b). Tetraploid.
NOTE BY C. R. FRASER-JENKINS: Previously reported by Mehra & Khullar (1980) etc. sub *P. setiferum* or *P. nigropalaeceum* as both diploid sexual and tetraploid sexual and it seems likely that a complex is involved. The diploid plant appears to have slightly smaller and more obtuse pinnules and fewer fibrillae on the rachis. The name *P. setiferum* and *P. nigropaleaceum* have previously been misapplied to this species.

50. *Polystichum lentum* (D. Don) Moore
CRFJ 7153: 1350 m, Narainkoti, Mandakini valley, N. of Rishikesh, Chamoli, Uttar Pradesh, N. India, 15 Sept. 1977. 2n = 82 (Figs 65a, b).
CRFJ 7154: as *CRFJ* 7153. Meiosis, 41 bivalents.
CRFJ 7155: as *CRFJ* 7153. Meiosis, 41 bivalents. (Figs 66a, b; 67a, b). Sexual diploid.
A previous diploid count was published by Verma (in Mehra, 1961).

51. *Polystichum makinoi* (Tagawa) Tagawa
CRFJ 9874: 1900 m Yu-Shien-Sze temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 164. Tetraploid.
Previous tetraploid counts for *P. makinoi* from Japan are by Kurita (1966) and Mitui (1968).

52. ? *P. pseudo-makinoi* Tagawa
CRFJ 9929: 1700 m between Chao-Lao-Dung and Yu-Shien-Sze, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82 (Figs 68a, b). Diploid.
This species from Japan (Mitui, 1968) is reported as tetraploid.
NOTE BY C. R. FRASER-JENKINS: This species has not yet been properly identified by the present authors and will be studied later. It is similar to *P. makinoi*, but slightly smaller and with slightly less lobed basal pinnules on each pinna. The stipe base scales are narrower than in *P. makinoi* but, as in that species, the sori are submarginal.

53. *P. xiphophyllum* (Baker) Diels
CRFJ 9921: 1500 m between Hong-Chun-Ping and Chao-Lao-Dung, Mt of 1000 temples, Omei Shan, Szechuan, China, 12 April 1980. 2n = 123. (Figs 69a, b). Triploid apomict.

54. *Polystichum nepalense* (Sprengel) C.Chr.
CRFJ 6792: 2500 m above Manali, Rohtang Pass, nr Kulu, Himachal Pradesh, NW. India, 2 Sept. 1977. Meiosis, 41 bivalents (Figs 70a, b).
CRFJ 6795: as *CRFJ* 6792. Meiosis, 41 bivalents. Sexual diploid.
A diploid count for this species is reported by Verma (in Mehra, 1961).

55. *Polystichum manmeiense* (Christ) Nakaike
CRFJ 10362: 3300 m between Sandakphoo and Kalpokhri, Singalilla Ridge, nr Darjeeling, W. Bengal, India. 21 Oct. 1980. 2n = 164. Tetraploid.
NOTE BY C. R. FRASER-JENKINS: This species has previously been known as *P. nepalense* var. *subbipinnatum* C.Chr., but being a distinct species, has been somewhat confused in recent publications. The cytology also supports the distinction from *P. nepalense* at specific rank. *P. falcatipinnum* Hayata from Taiwan is synonymous.

56. *Polystichum neolobatum* Nakai
CRFJ 7530: 3000 m Mt Hattu, Narkanda, nr Simla, Himachal Pradesh, N. India, 26 Aug. 1978. 2n = *c.*121. Triploid apomict.
This confirms a previous report on Japanese material by Daigobo (1973).
NOTE BY C. R. FRASER-JENKINS: Previously known in India as *P. garhwalicum* or largely overlooked.

57. *Polystichum semifertile* (Clark) Ching
CRFJ 10372: 1800 m Lebong forest, N. of Darjeeling, W. Bengal, India, 25 Oct. 1980. 2n = 82.
CRFJ 10373: as *CRFJ* 10372. 2n = 82. Diploid.
A diploid count for this species is reported by Verma (*in* Mehra, 1961).

58. *Polystichum squarrosum* (D. Don) Fée
CRFJ 6955: 1500 m Naini Khad, Dalhousie, Himachal Pradesh, NW. India, 30 Aug. 1977. 2n = *c.*80.
CRFJ 6972: 2400 m Matiana, between Simla and Narkanda, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 82. Diploid.
This confirms previous reports by Verma & Loyal (1960), Verma (*in* Mehra, 1961) and Khullar & Gupta (1978).
NOTE BY C. R. FRASER-JENKINS: Due to a photograph of *P. neolobatum* erroneously labelled as the type of *P. squarrosum* at Peking, Ching has for many years misapplied the name to specimens of *P. neolobatum* with wider pinnules. True *P. squarrosum* is rare in SE. Tibet and does not occur in China.

59. *Polystichum tsus-simense* (Hook.) J. Smith
CRFJ 9872: 1900 m Yu-Shien Sze temple, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 123.
CRFJ 9940: 950 m Wu-Shien-Kang, Mt of 1000 temples, Omei Shan, Szechuan, China, 11 April 1980. 2n = 123 (Figs 71a, b).
CRFJ 9999: 2250 m Tai-Hwa-Sze temple, Zhi Shan, W. of Kunming, Yunnan, China, 17 April 1980. 2n = 123 (Figs 72a, b). Triploid apomict.
P. tsus-simense from Japen is reported as triploid apomict by Mitui (1965, 1968), Hirabayashi (1969), and Daigobo (1973).
NOTE BY C. R. FRASER-JENKINS: This species is extremely close to, or perhaps synonymous with the W. Himalayan and S. African *P. luctuosum* (Kunze) T. Moore, and may represent little more than a vicariant taxon, a situation common to a number of other W. Himalayan species.

60. *Polystichum chunii* Ching
CRFJ 10369 1800 m Lebong forest, N. of Darjeeling, W. Bengal, India, 25 Oct. 1980. 2n = *c.*82. Diploid.
NOTE BY C. R. FRASER-JENKINS: Reported from the Indian subcontinent for the first time here. This species is somewhat intermediate between *P. lentum* and *P. semifertile* and has a narrow frond usually with an apical bud, but larger pinnae than *P. lentum* and with more and smaller pinnules.

61. *Polystichum yunnanense* Christ
CRFJ 9998: 2250 m Tai-Hwa-Sze temple, Zhi Shan, W. of Kunming, Yunnan, China, 17 April 1980. 2n = 164 (Figs 73a, b). Tetraploid.
NOTE BY C. R. FRASER-JENKINS: Christ reported this species from the Indo-Himalaya as well as from Yunnan. However, the Yunnan plant appears to be a distinct species and is slightly different from the Himalayan plant, *P. piceo-paleaceum* Tagawa (see sub. 49). The whole *P. yunnanense* and *P. makinoi* complex requires further taxonomic study.

62. *Polystichum omeiense* C.Chr.
CRFJ 9943: 950 m 3 km above Wu-Shien-Kang, NE. side of Mt of 1000 temples, Omei Shan, Szechuan, China, 11 April 1980. 2n = 82; meiosis, 41 bivalents. Diploid sexual.

Other genera

63. *Diacalpe christensenii* Ching
CRFJ 10021: 2100 m Ching-Chu-Sze temple, N. Zhi Shan, NW. of Kunming, Yunnan, China, 17 April 1980. 2n = 82. Diploid.

64. *Ctenitis mariformis* (Rosenst.) Ching
CRFJ 9870: 1800 m Wan-Nian-Sze, Mt of 1000 temples, Omei Shan, Szechuan, China, 13 April 1980. 2n = 82 (Figs 74a, b). Diploid.

65. *Hypodematium crenatum* (Forsskal) Kuhn agg.
CRFJ 10015: 2250 m. Tai-Hwa-Sze, Zhi Shan, W. of Kunming, Yunnan, China, 17 April 1980. 2n = 164 (Figs 75a, b). Tetraploid.
Previous reports of this species from India by Mehra & Loyal (1965) and Roy, Sinha & Sakya (1971) describe it as a diploid sexual species. This tetraploid from China has pinkish costae and a slightly less dissect lamina, and must represent a separate taxon. A tetraploid sexual taxon and a sterile triploid hybrid have also been discovered in India by Loyal (in prep.).

66. *Asplenium adiantum-nigrum* L.
CRFJ 6912: 1700 m Baragran, Kulu to Manali, Himachal Pradesh, NW. India, 4 Sept. 1977. 2n = *c.*140. Tetraploid.
This species was first reported by Manton (1950) from Europe, where it is also tetraploid.

67. *Asplenium laciniatum* Don agg.
CRFJ 6902: as *CRFJ* 6912 above. 2n = *c.*140. Tetraploid.
The presence of bad spores indicates that this specimen is a hybrid; its morphology shows affinities with the *A. laciniatum* Don (= *A. varians*) agg. Unfortunately the plant died before meiosis could be studied.

68. *Aleuritopteris albo-marginata* (Clarke) Ching
CRFJ 6959: 2450 m E. of Simla on Narkanda road, Himachal Pradesh, NW. India, 6 Sept. 1977. 2n = 58 (Figs 76a, b; 77a, b). Diploid.
This agrees with an earlier count by Verma (in Mehra, 1961).

69. *Neocheiropteris palmato-pedata* (Baker) Christ
CRFJ 10017: 2250 m Tai-Hwa-Sze, Zhi Shan, W. of Kunming, Yunnan, China, 17 April 1980. 2n = *c.*70 (Figs 78a, b). Diploid.

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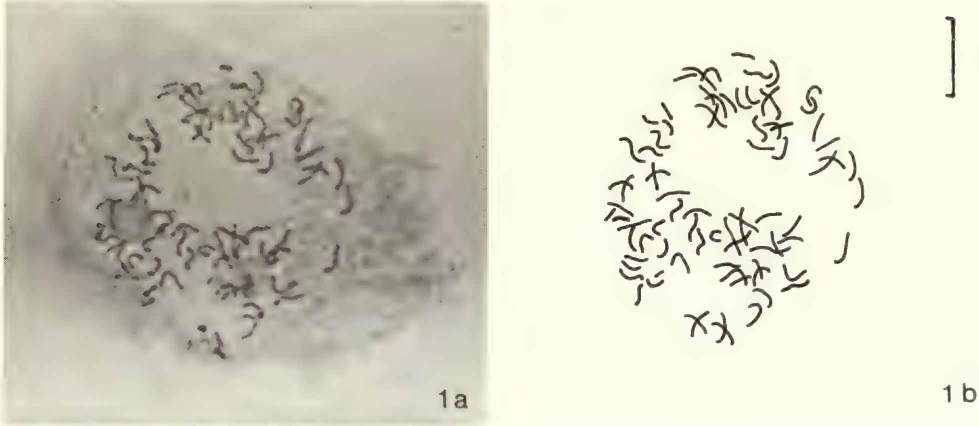
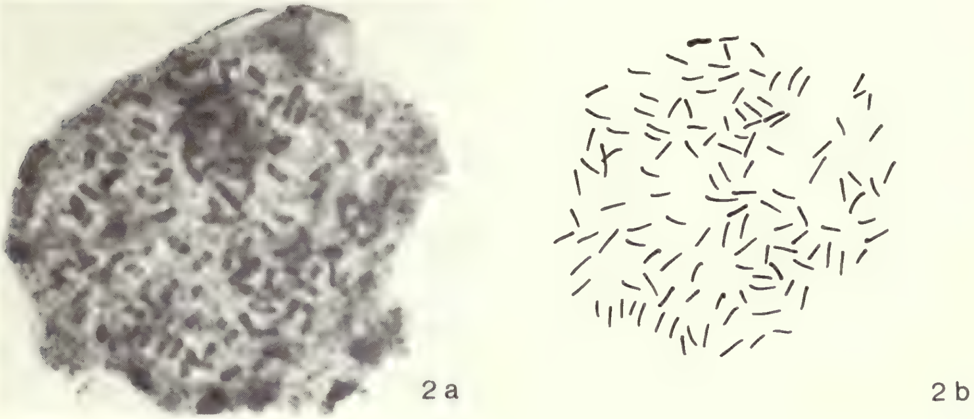
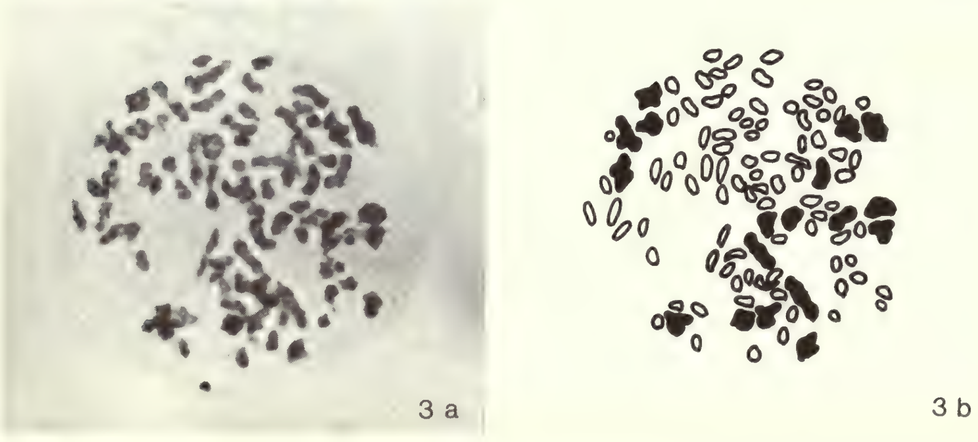


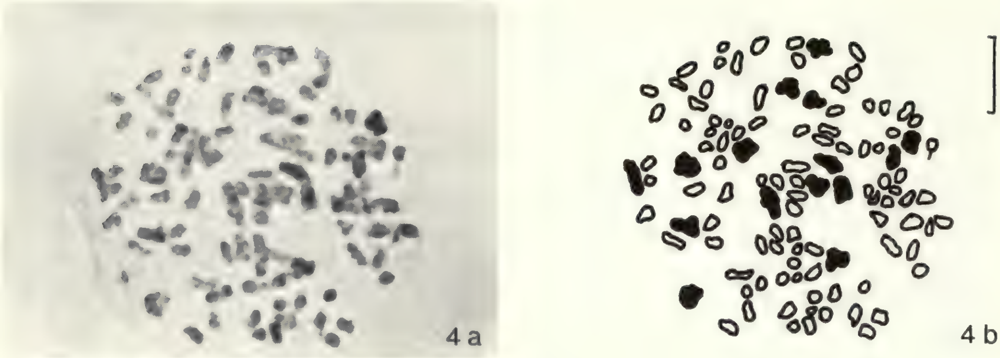


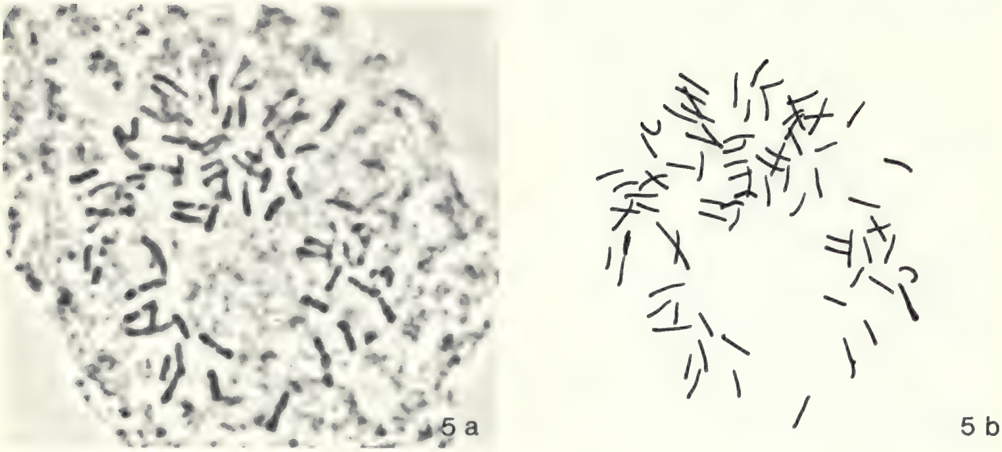


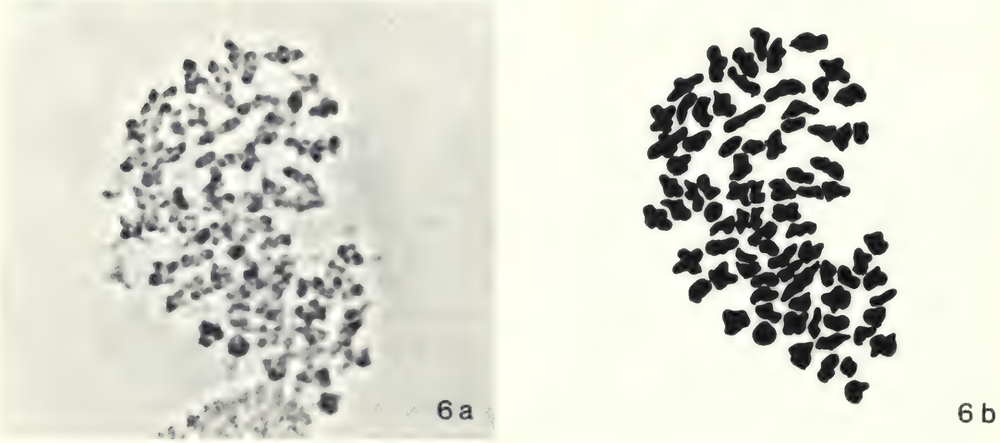
Figs 1a, b *Dryopteris podophylla, CRFJ* 10069: photograph and drawing of root tip mitosis showing 82 chromosomes. (Scale represents 10 μm throughout.)

Figs 2a, b *Dryopteris cycadina, CRFJ* 10491: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 3a, b *Dryopteris darjeelingensis, CRFJ* 8559: photograph and drawing of meiosis from a 16-celled sporangium showing 18 bivalents (in black) and 87 univalents (outlined).



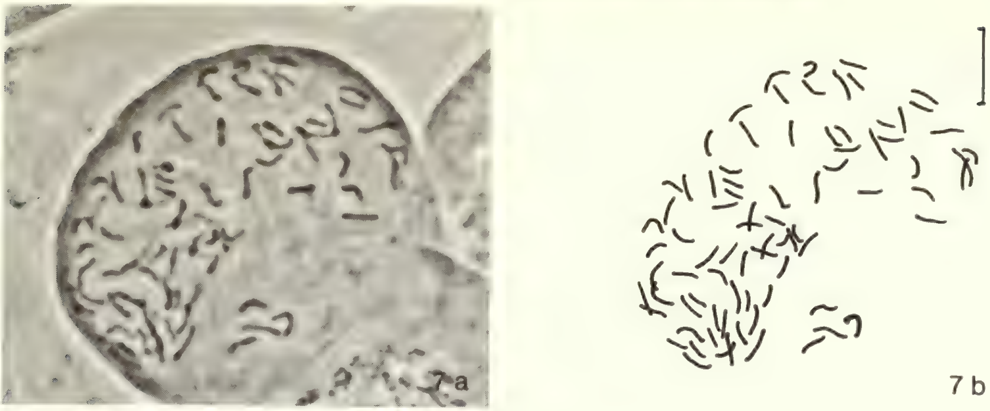


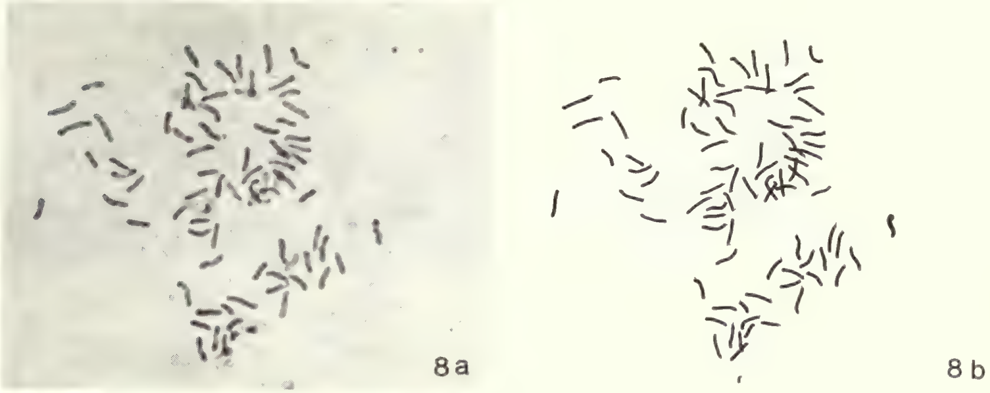


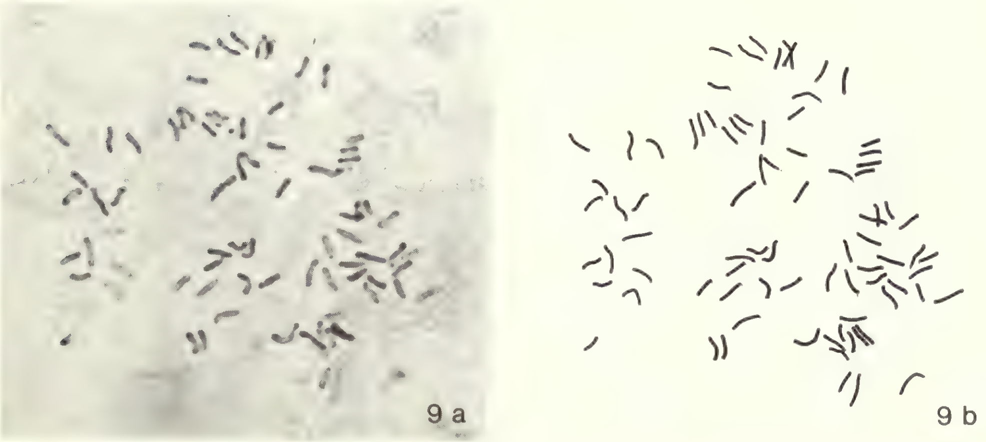
Figs 4a, b *Dryopteris darjeelingensis, CRFJ* 8559: photograph and drawing of meiosis from a 16-celled sporangium showing 15 bivalents (in black) and 93 univalents (outlined).

Figs 5a, b *Dryopteris stenolepis, CRFJ* 8820: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 6a, b *Dryopteris stenolepis, CRFJ* 8820: photograph and drawing of meiosis from an 8-celled sporangium showing 82 bivalents (in black).



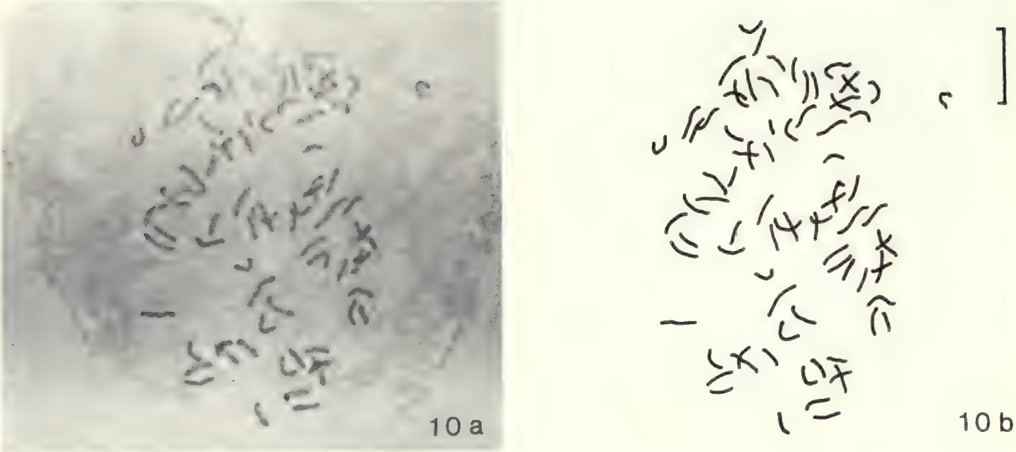


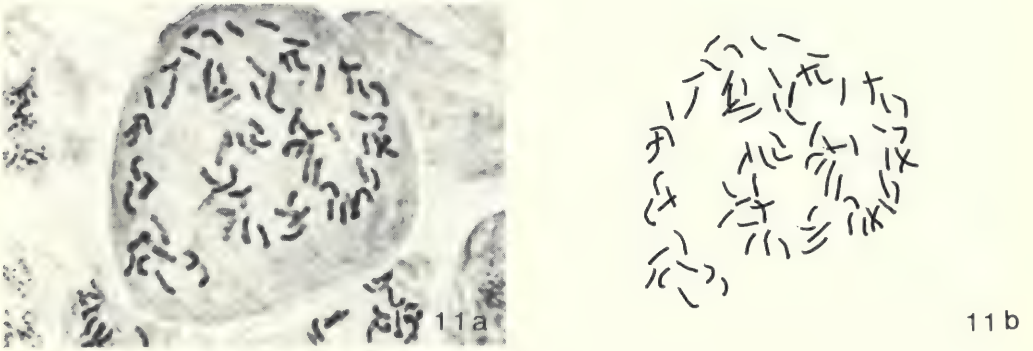


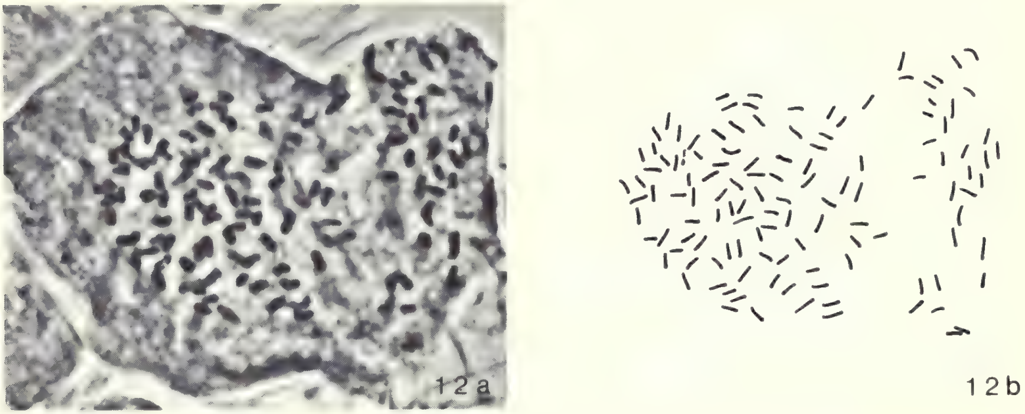
Figs 7a, b *Dryopteris stenolepis, CRFJ* 9933: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 8a, b *Dryopteris dickinsii, CRFJ* 9869: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 9a, b *Dryopteris dickinsii, CRFJ* 9968: photograph and drawing of root tip mitosis showing 82 chromosomes.



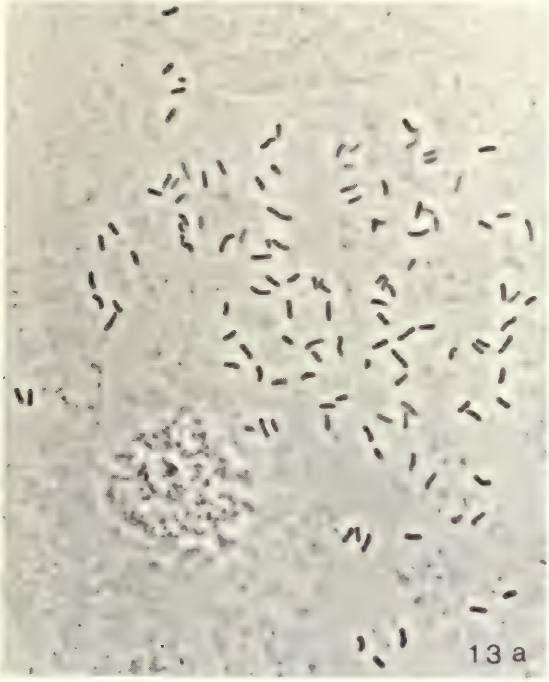


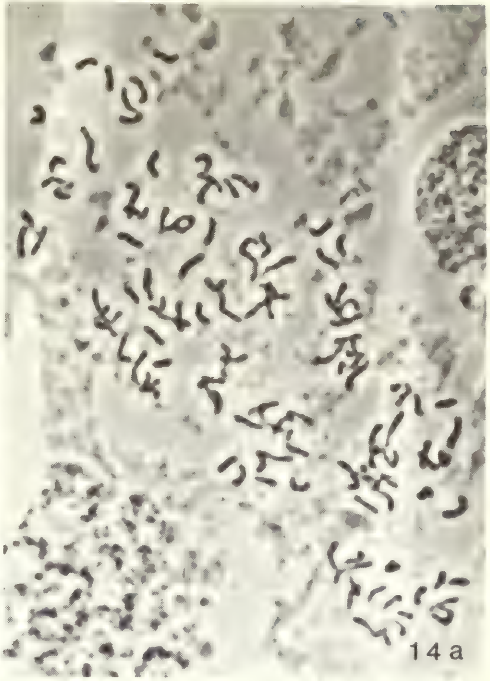


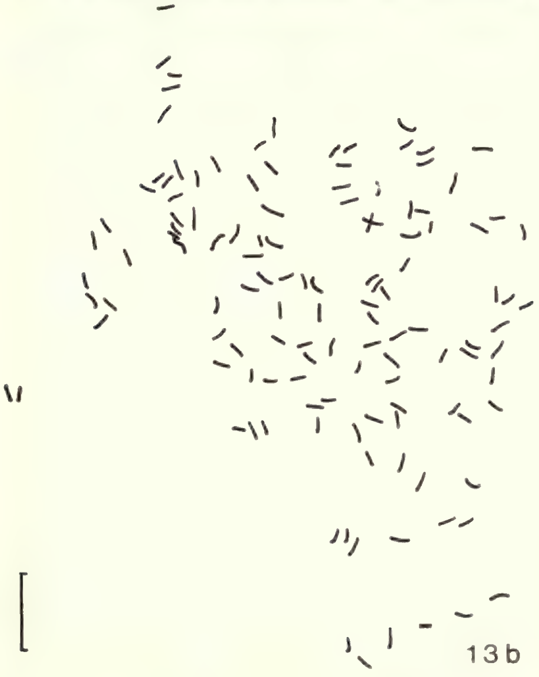
Figs 10a, b *Dryopteris dickinsii, CRFJ* 9969: photograph and drawing of root tip mitosis showing 82 chromosomes.

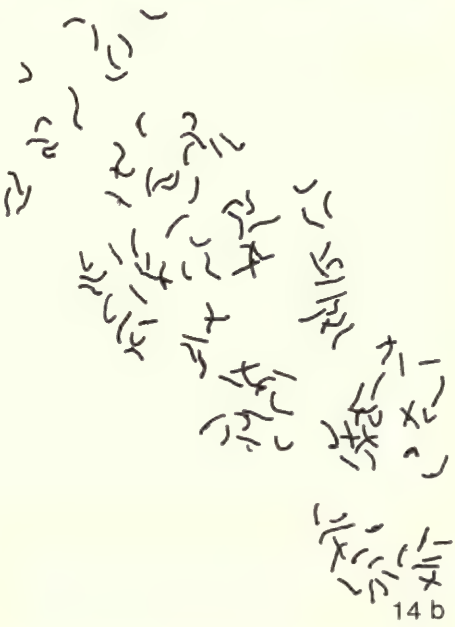
Figs 11a, b *Dryopteris rosthornii, CRFJ* 9926: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 12a, b *Dryopteris yigonensis*, *CRFJ* 7612: photograph and drawing of root tip mitosis showing 123 chromosomes.



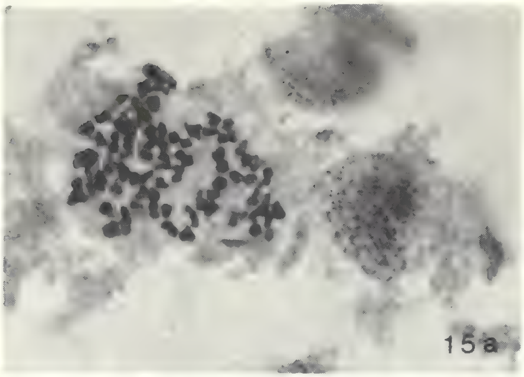




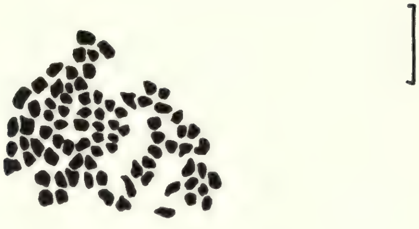


Figs 13a, b *Dryopteris yigonensis*, *CRFJ* 7647: photograph and drawing of root tip mitosis showing 123 chromosomes.

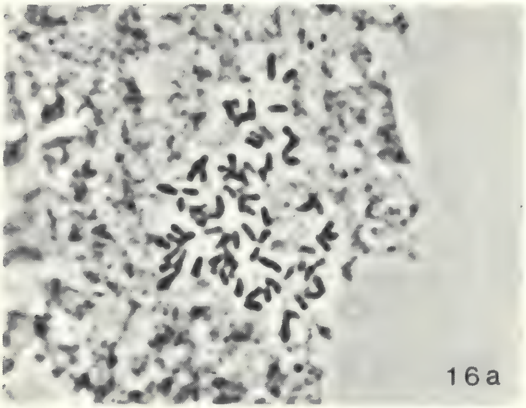
Figs 14a, b *Dryopteris yigonensis*, *CRFJ* 7657: photograph and drawing of root tip mitosis showing 123 chromosomes.



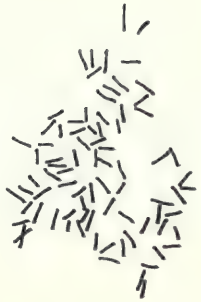
15a



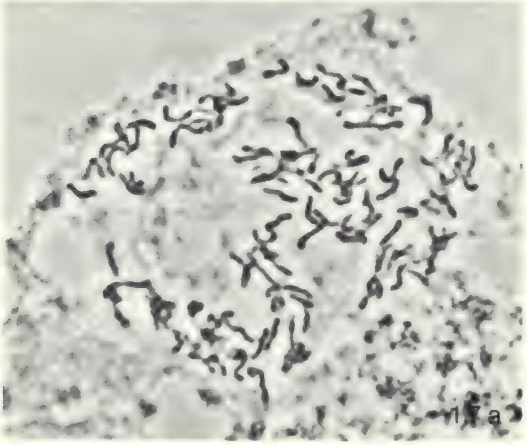
15b



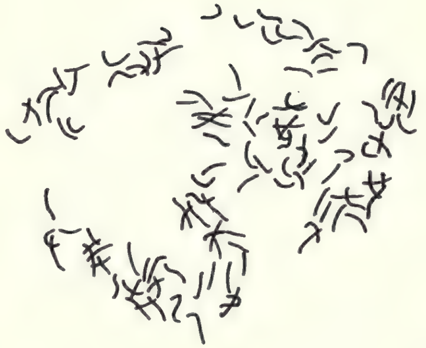
16a



16b



17a

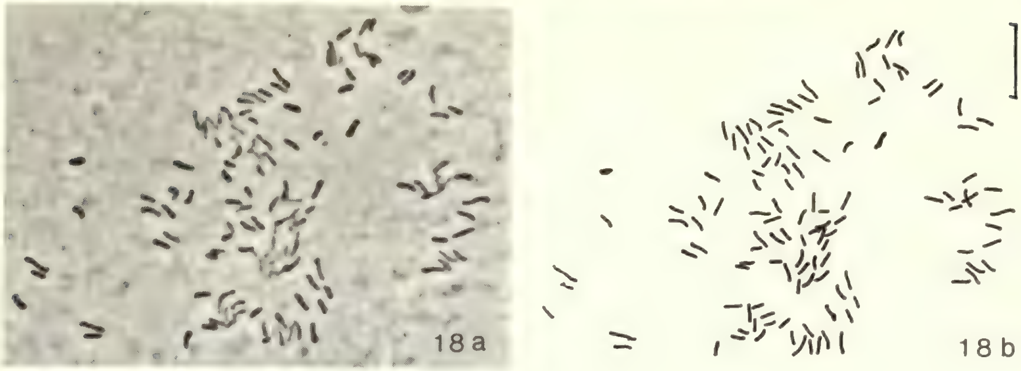


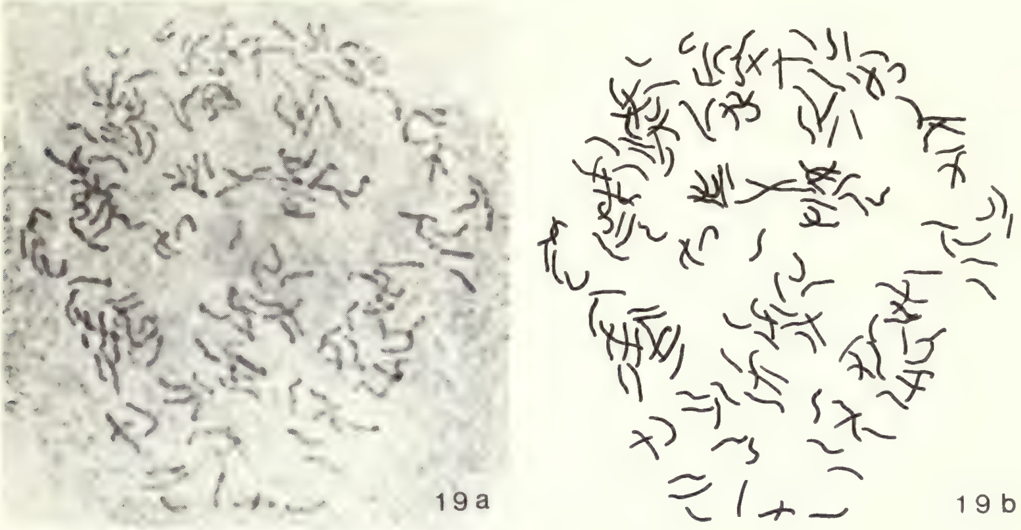
17b

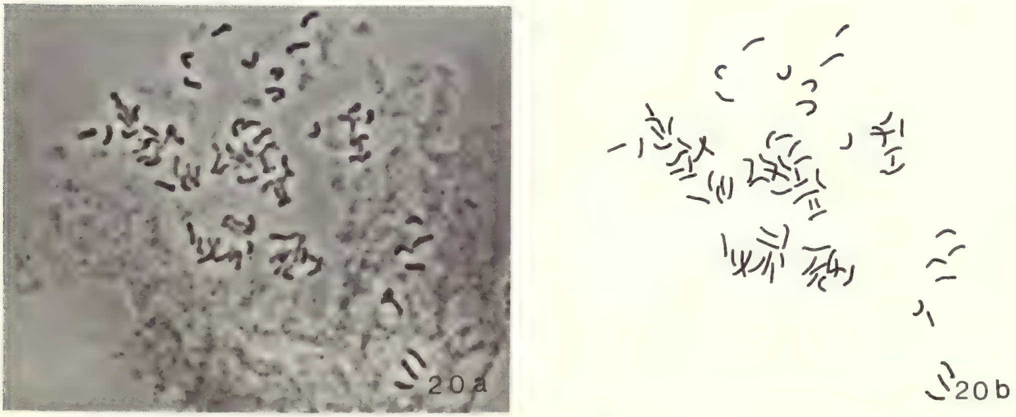
Figs 15a, b *Dryopteris lepidopoda, CRFJ* 9881: photograph and drawing of meiosis from an 8-celled sporangium showing 82 bivalents (in black).

Figs 16a, b *Dryopteris lepidopoda, CRFJ* 9927: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 17a, b *Dryopteris parrisiae, CPG* 3396: photograph and drawing of root tip mitosis showing 123 chromosomes.



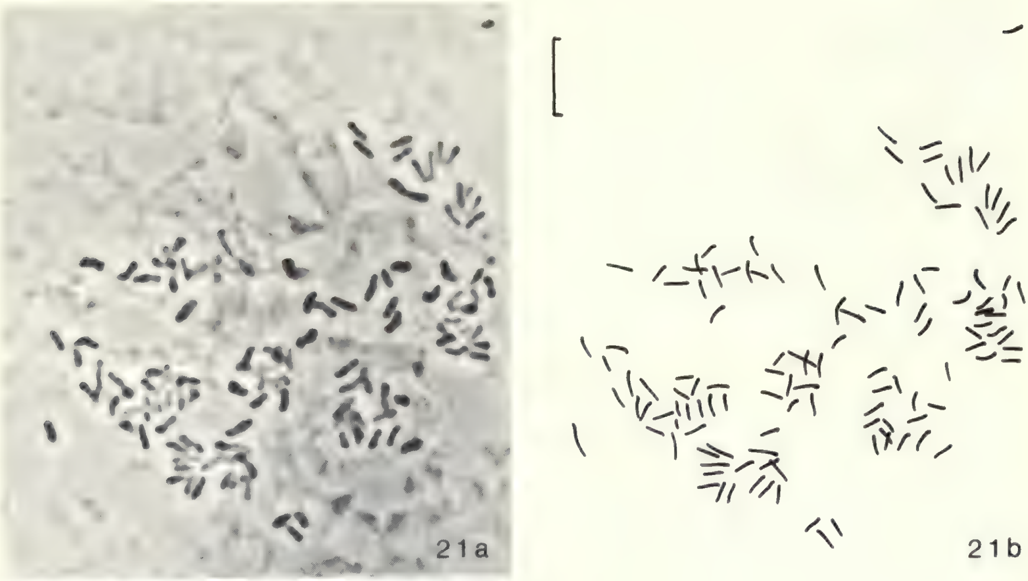


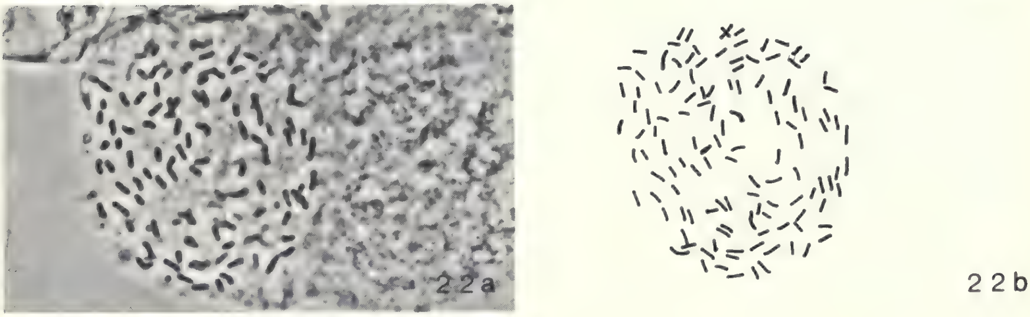


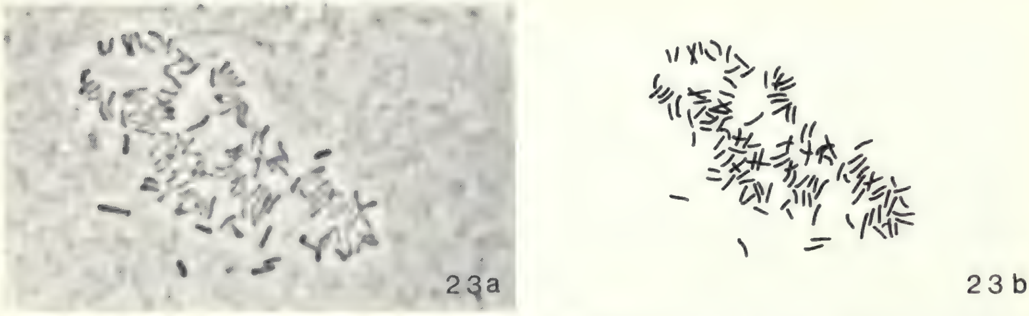
Figs 18a, b *Dryopteris madrasensis, CRFJ* 9205: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 19a, b *Dryopteris sledgei, CRFJ* 9351: photograph and drawing of root tip mitosis showing 164 chromosomes.

Figs 20a, b *Dryopteris chrysocoma, CRFJ* 6773: photograph and drawing of root tip mitosis showing 82 chromosomes.



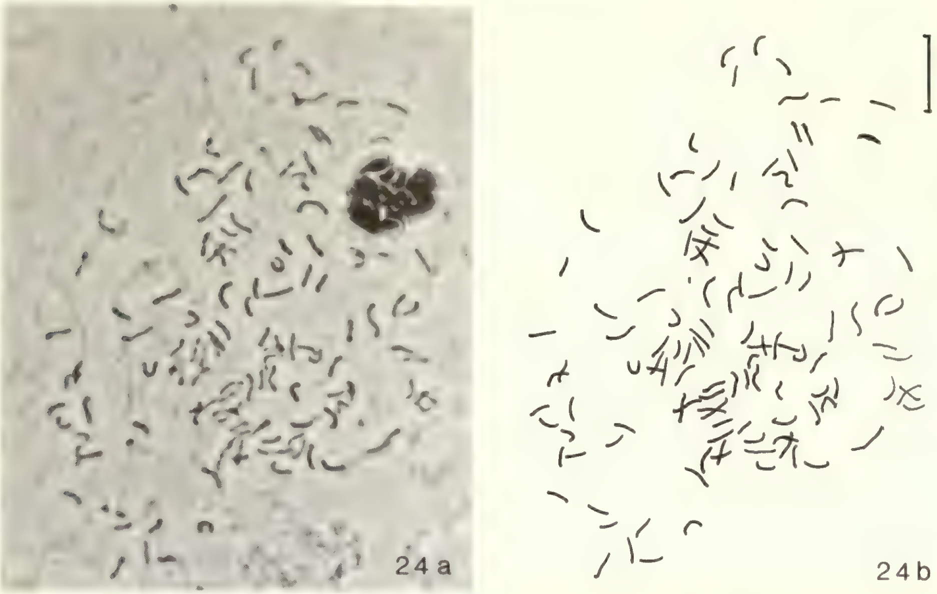


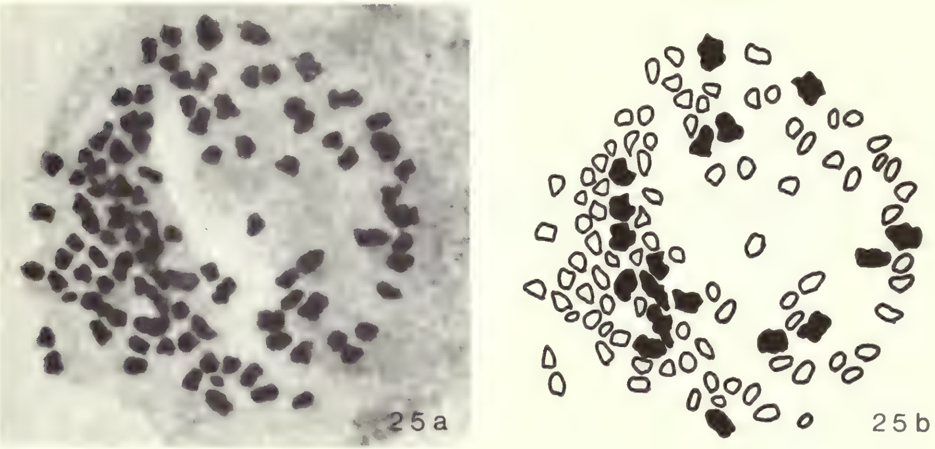


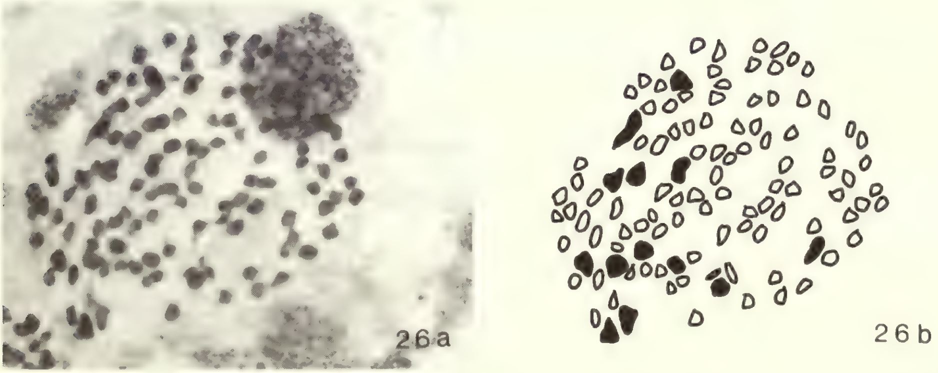
Figs 21a, b *Dryopteris blanfordii* subsp. *blanfordii, CRFJ* 6810: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 22a, b *Dryopteris blanfordii* subsp. *blanfordii, CRFJ* 7404: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 23a, b *Dryopteris sublacera, CRFJ* 7596: photograph and drawing of root tip mitosis showing 123 chromosomes.



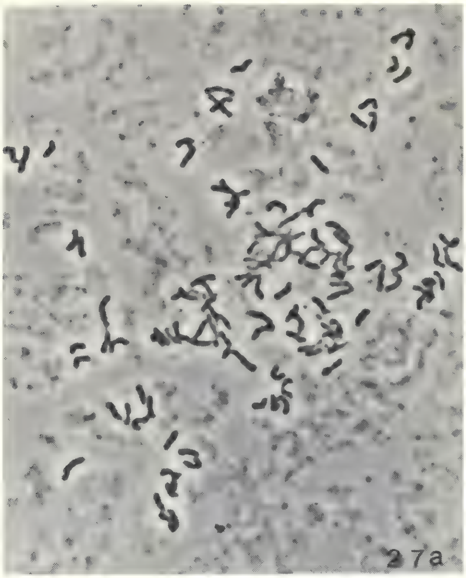


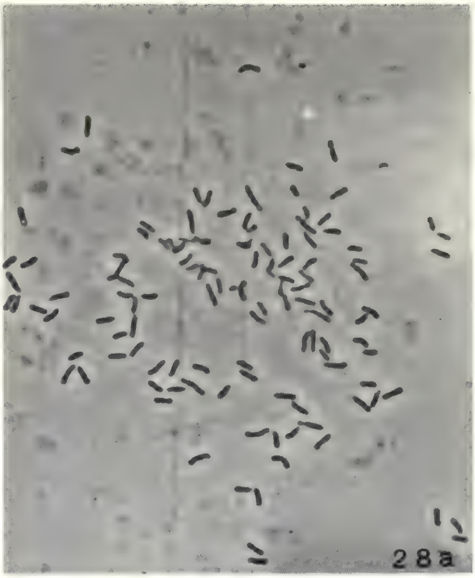


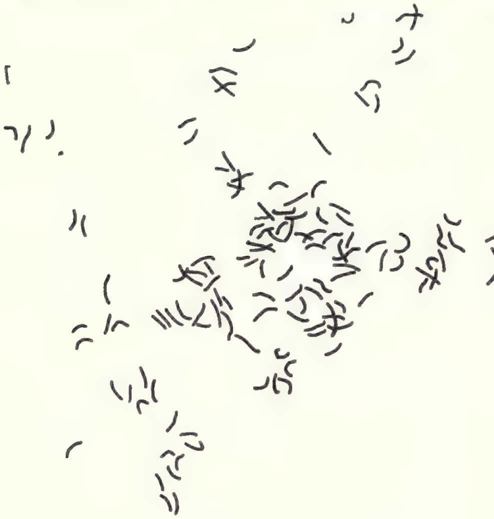
Figs 24a, b *Dryopteris sublacera, CRFJ* 9988: photograph and drawing of root tip mitosis showing 123 chromosomes.

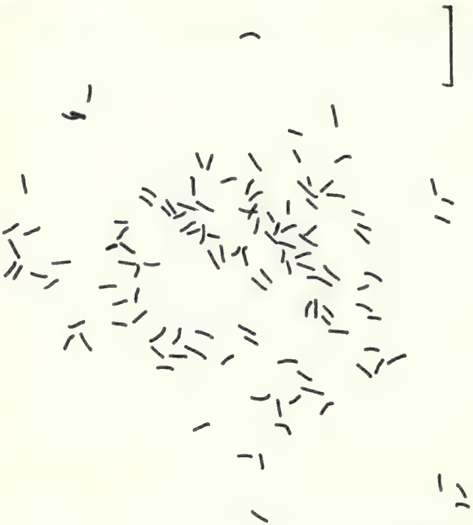
Figs 25a, b *Dryopteris odontoloma, CRFJ* 9318: photograph and drawing of meiosis from a 16-celled sporangium showing 18 bivalents (in black) and 87 univalents (outlined).

Figs 26a, b *Dryopteris odontoloma, CRFJ* 9318: photograph and drawing of meiosis from a 16-celled sporangium showing 13 bivalents (in black) and 97 univalents (outlined).



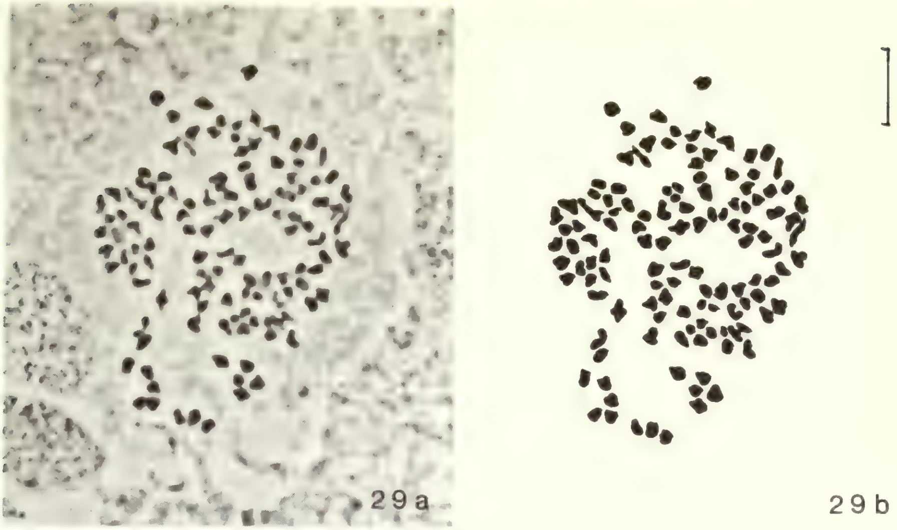


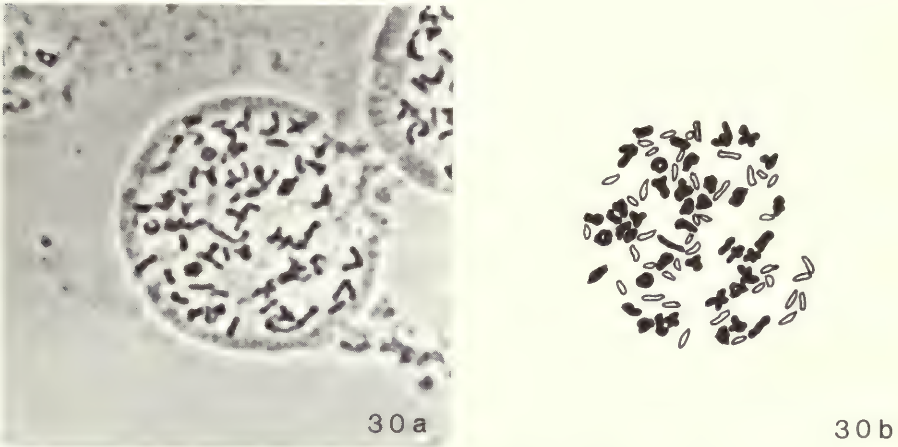




Figs 27a, b *Dryopteris juxtaposita, CRFJ* 6995: photograph and drawing of root tip mitosis showing 123 chromosomes.

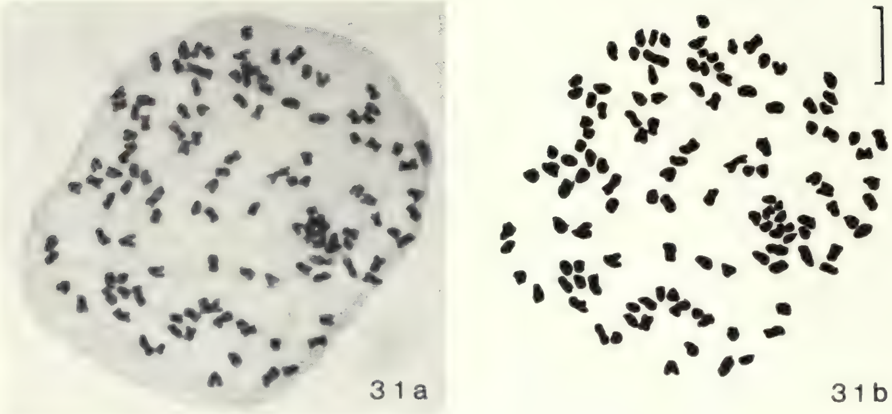
Figs 28a, b *Dryopteris juxtaposita, CRFJ* 7241: photograph and drawing of root tip mitosis showing 123 chromosomes.

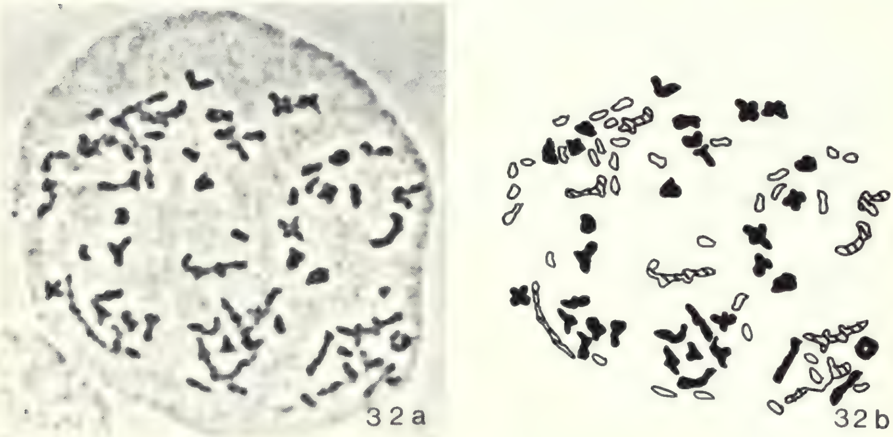


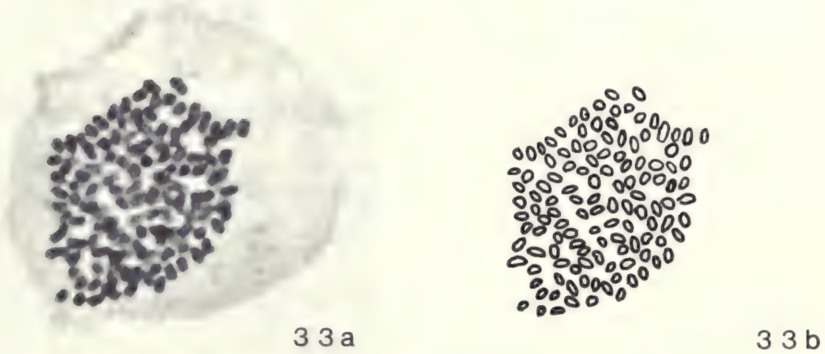


Figs 29a, b *Dryopteris juxtaposita, CRFJ* 7163: photograph and drawing of meiosis from an 8-celled sporangium showing 123 bivalents (in black).

Figs 30a, b *Dryopteris juxtaposita, CRFJ* 7163: photograph and drawing of meiosis from a 16-celled sporangium showing 41 bivalents (in black) and 41 univalents (outlined).



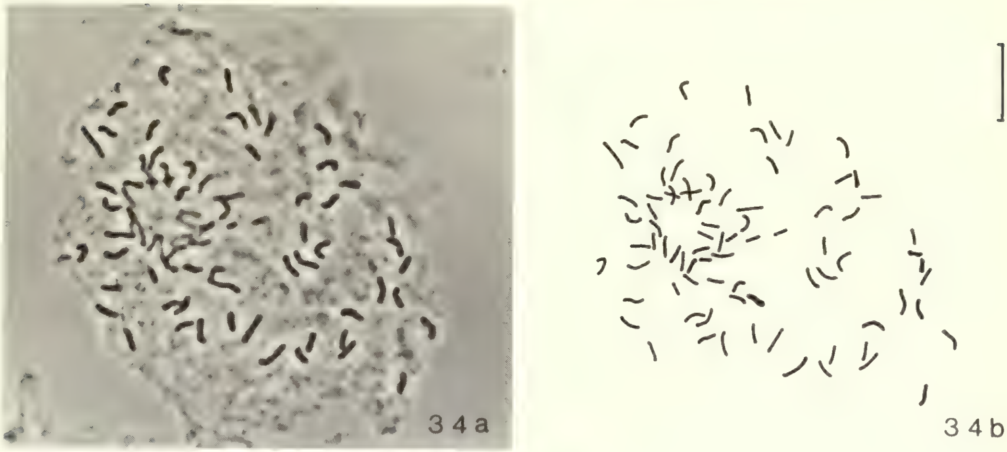


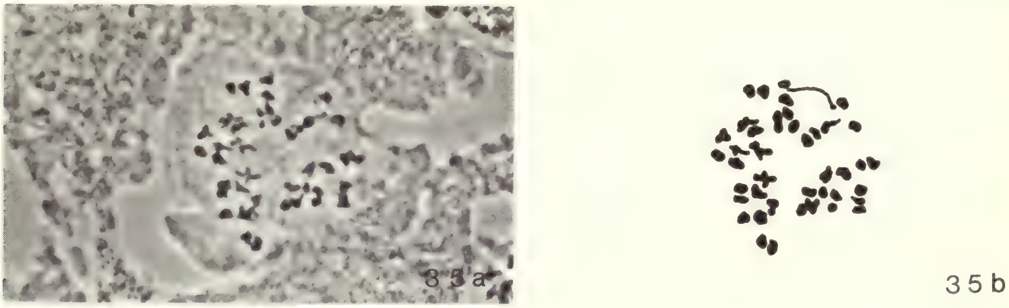


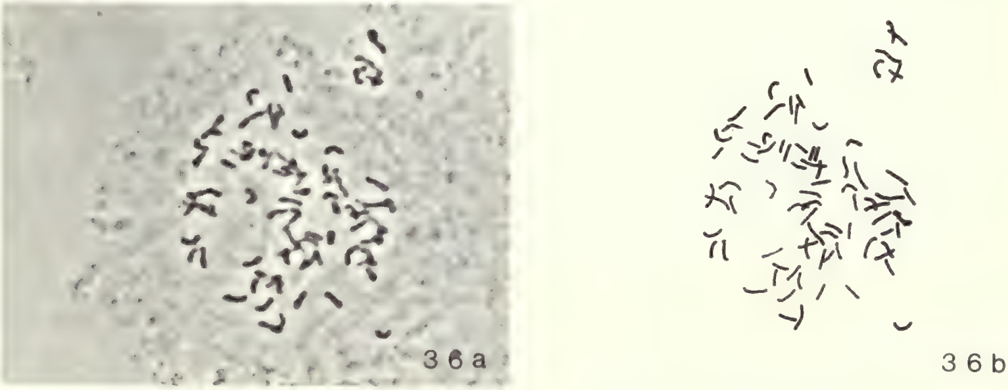
Figs 31a, b *Dryopteris juxtaposita, TR* 4590: photograph and drawing of meiosis from an 8-celled sporangium showing 123 bivalents (in black).

Figs 32a, b *Dryopteris juxtaposita, TR* 4590: photograph and drawing of meiosis from a 16-celled sporangium showing 8 trivalents (striped), 33 bivalents (in black), and 33 univalents (outlined).

Figs 33a, b *Dryopteris juxtaposita, CRFJ* 9894: photograph and drawing of meiosis from a 16-celled sporangium showing *c.* 123 univalents (outlined).



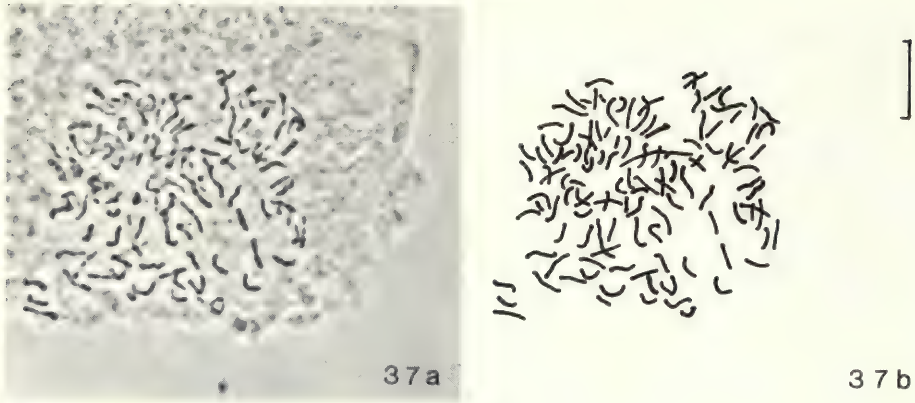


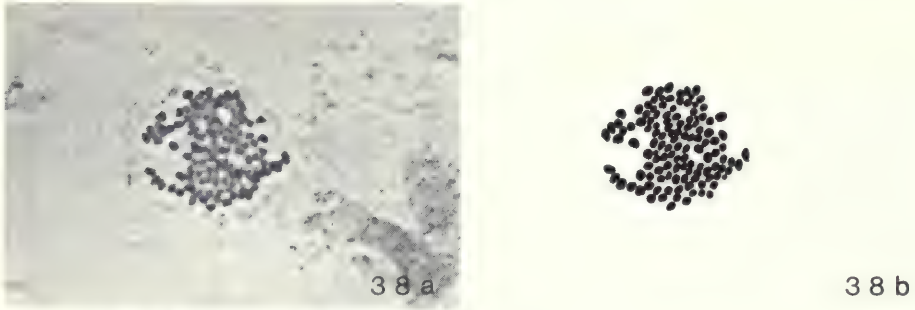


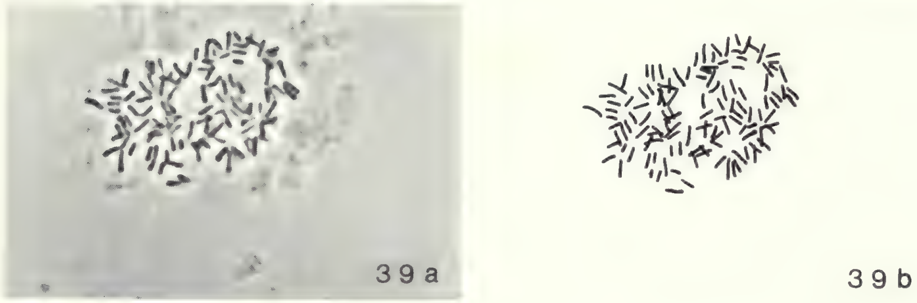
Figs 34a, b *Dryopteris nigropaleacea, CRFJ* 6925: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 35a, b *Dryopteris nigropaleacea, CRFJ* 6933: photograph and drawing of meiosis showing 41 bivalents (in black).

Figs 36a, b *Dryopteris nigropaleacea, CRFJ* 6990: photograph and drawing of root tip mitosis showing 82 chromosomes.



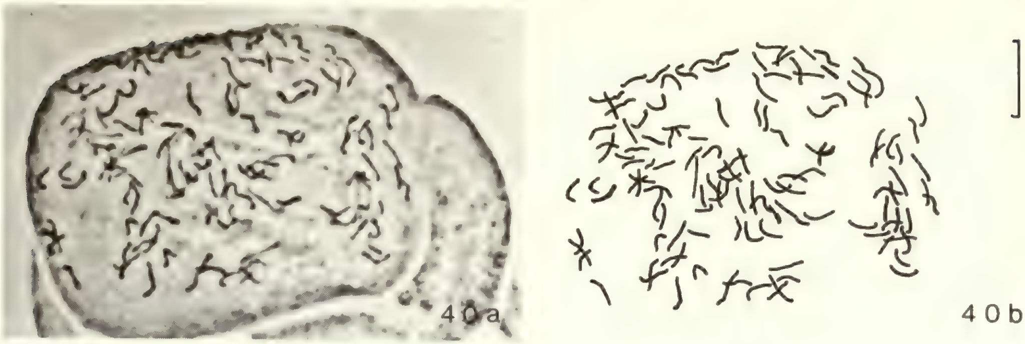


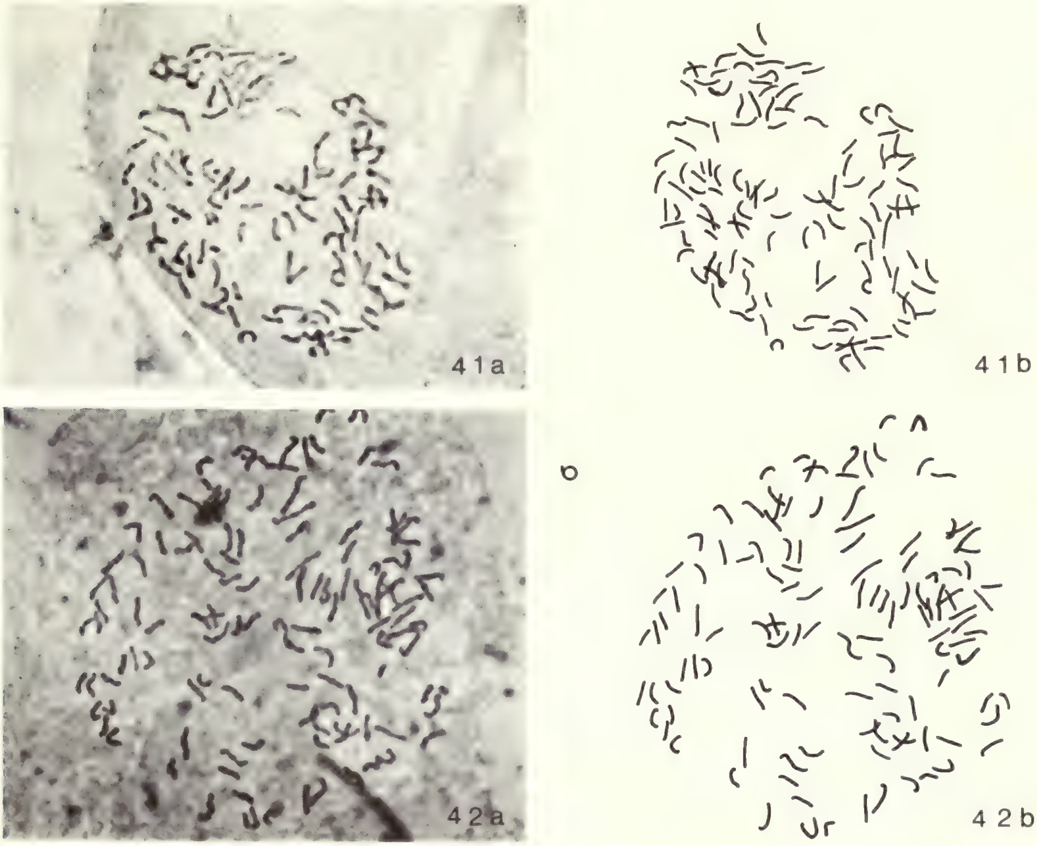


Figs 37a, b *Dryopteris stewartii, CRFJ* 6332: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 38a, b *Dryopteris stewartii, CRFJ* 6804: photograph and drawing of meiosis from an 8-celled sporangium showing *c.*123 bivalents (in black).

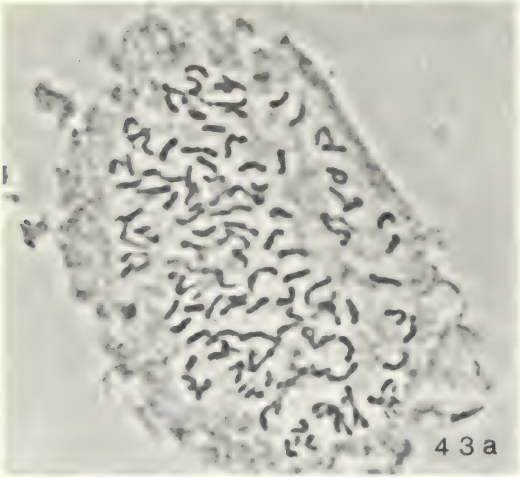
Figs 39a, b *Dryopteris stewartii, CRFJ* 6970: photograph and drawing of root tip mitosis showing 123 chromosomes.

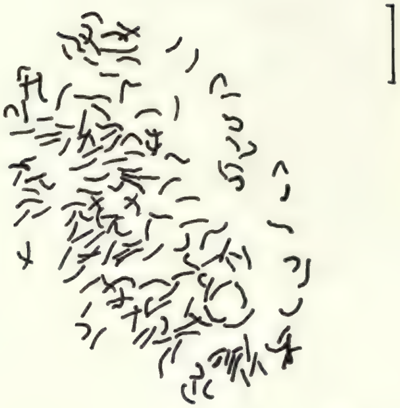




Figs 40a, b *Dryopteris fructuosa, CRFJ* 9996: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 41a, b; 42a, b *Dryopteris basisora, CRFJ* 9986: photograph and drawing of root tip mitosis showing 123 chromosomes.


4 3 a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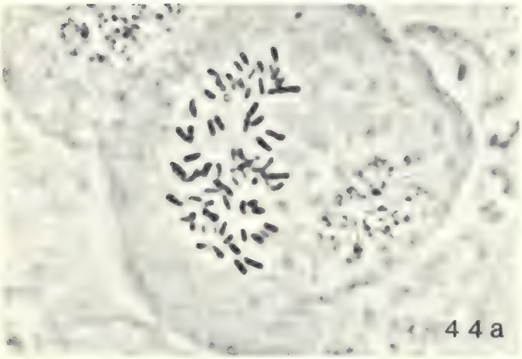
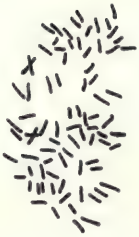

4 4 a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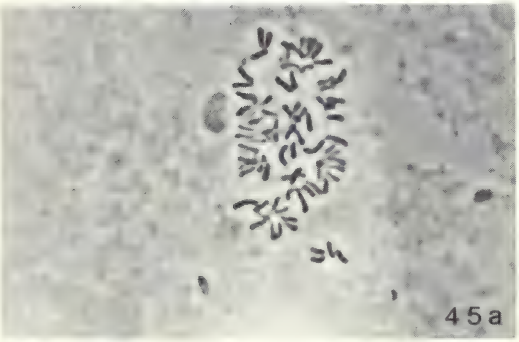
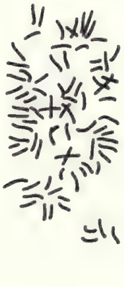
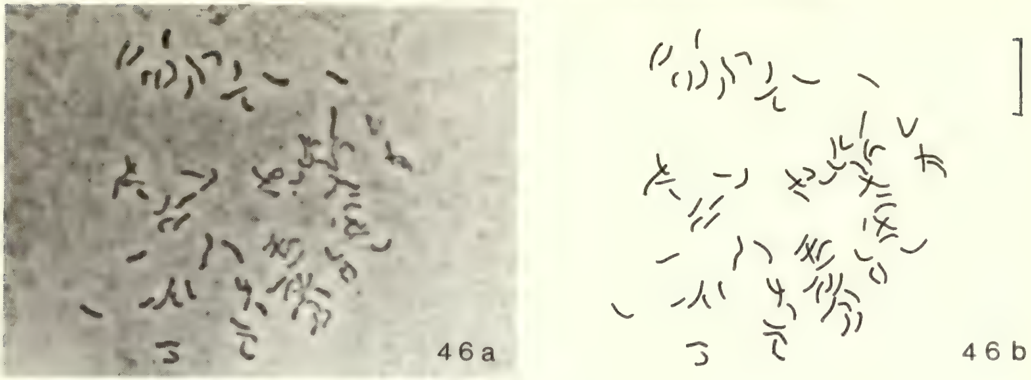

4 5 a

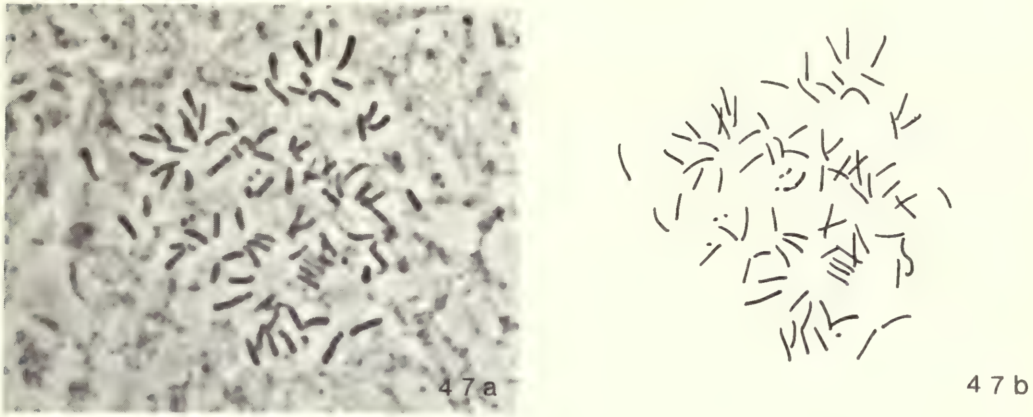

4 5 b

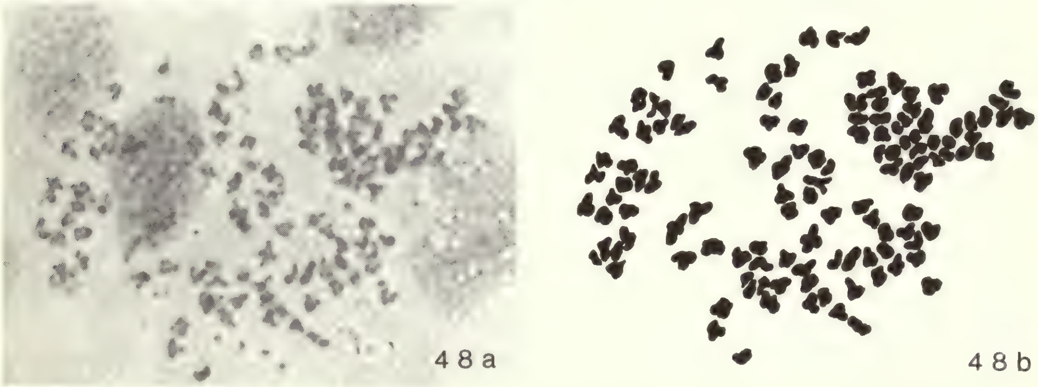
Figs 43a, b *Dryopteris pteridiiformis, CRFJ* 10028: photograph and drawing of root tip mitosis showing 164 chromosomes.

Figs 44a, b *Dryopteris subimpressa, CRFJ* 7217: photograph and drawing of root tip mitosis showing *c.*82 chromosomes.

Figs 45a, b *Dryopteris caroli-hopei, CRFJ* 7062: photograph and drawing of root tip mitosis showing 82 chromosomes.



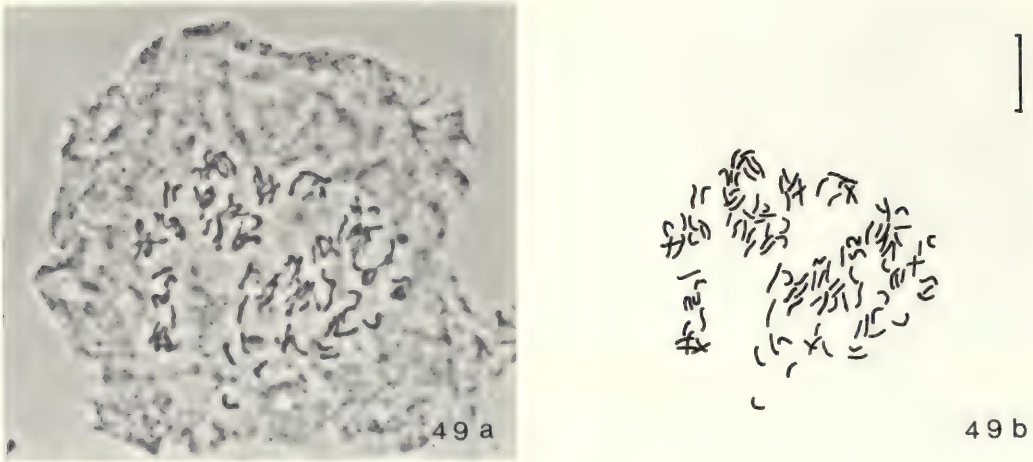


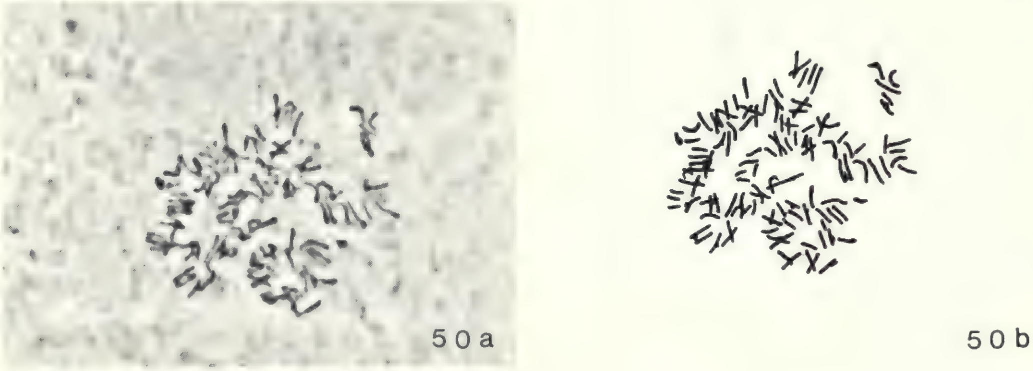


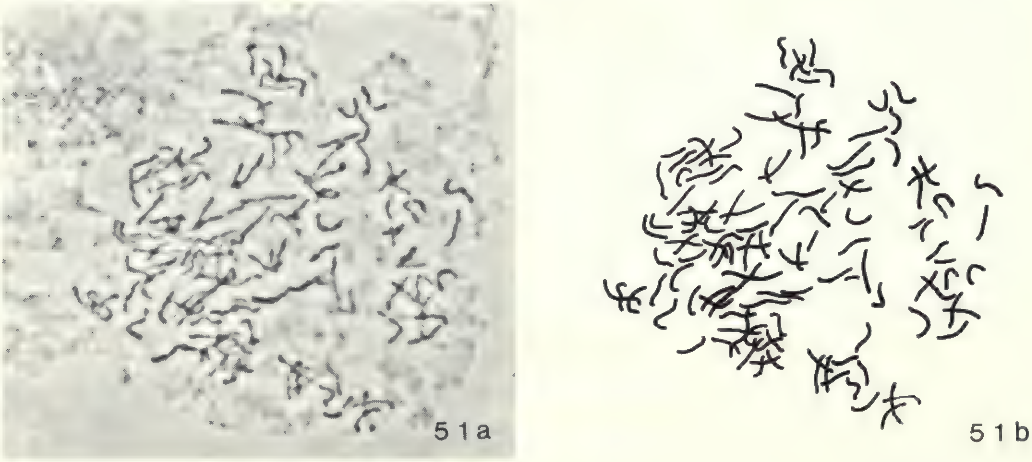
Figs 46a, b *Dryopteris caroli-hopei, CRFJ* 7159: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 47a, b *Dryopteris porosa, CRFJ* 9887: photograph and drawing of root tip mitosis showing *c.*82 chromosomes.

Figs 48a, b *Dryopteris subtriangularis, CRFJ* 9897: photograph and drawing of meiosis from an 8-celled sporangium showing 123 bivalents (in black).



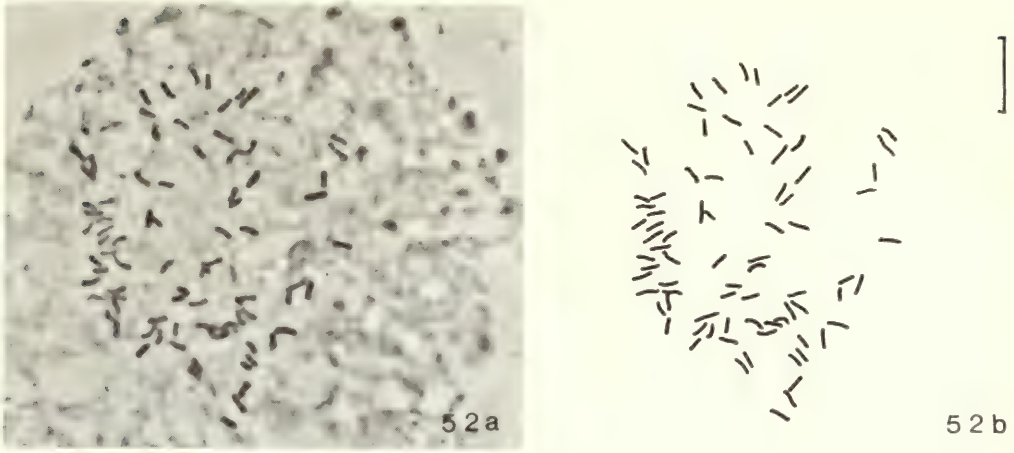


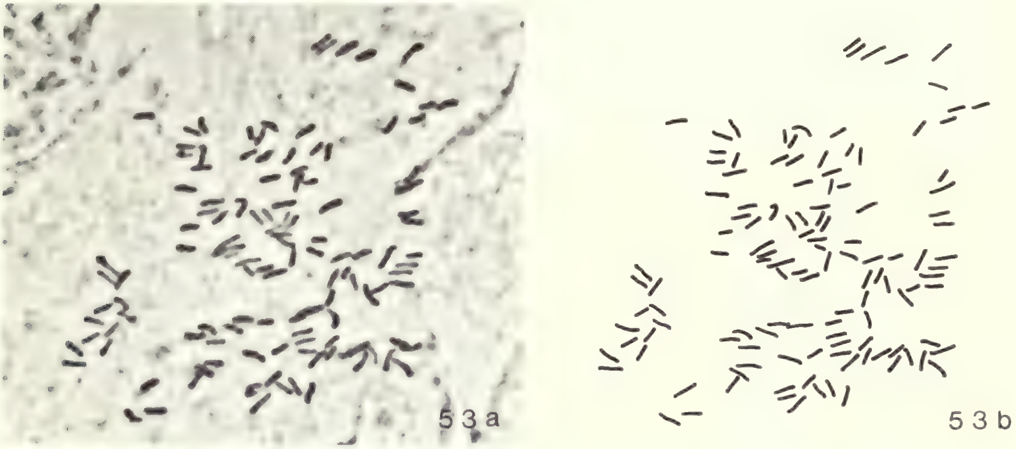


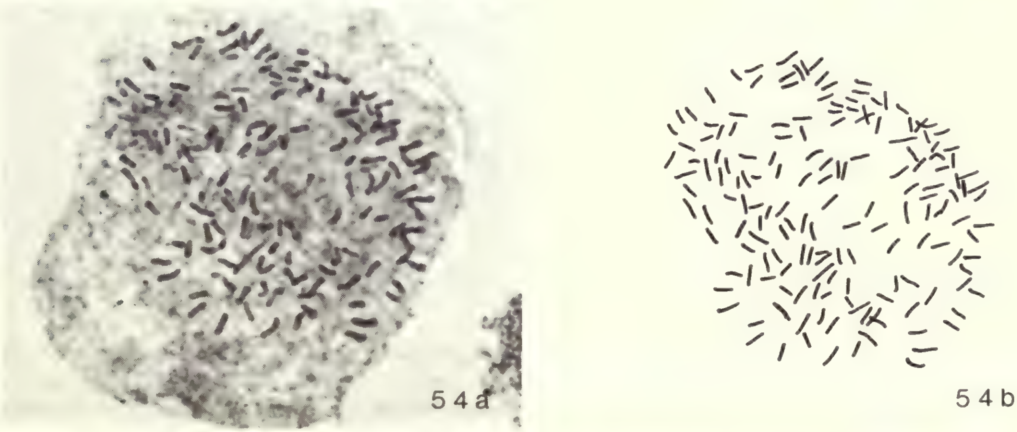
Figs 49a, b *Dryopteris gymnosora, CRFJ* 9939: photograph and drawing of root tip mitosis showing 123 chromosomes.

Figs 50a, b *Dryopteris integriloba, CRFJ* 10065: photograph and drawing of root tip mitosis showing *c.* 120 chromosomes.

Figs 51a, b *Dryopteris integriloba, CRFJ* 10067: photograph and drawing of root tip mitosis showing *c.* 123 chromosomes.



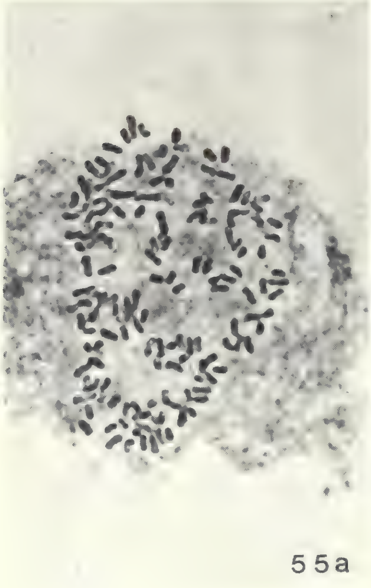




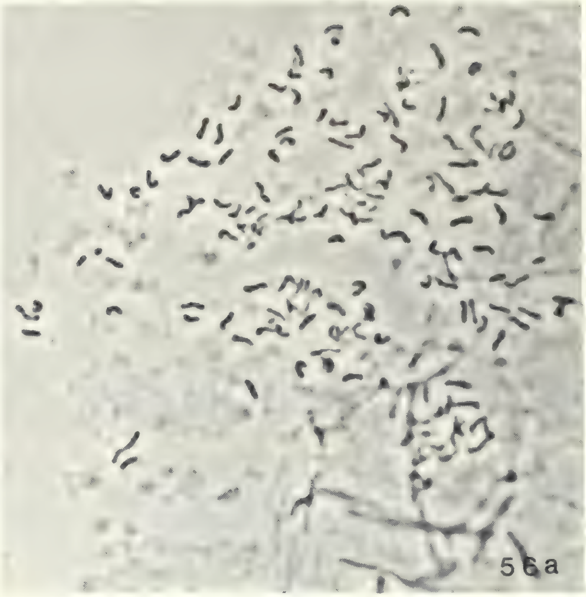
Figs 52a, b *Dryopteris championii, CRFJ* 10056: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 53a, b *Dryopteris varia, CRFJ* 10054: photograph and drawing of root tip mitosis showing 123 chromosomes.

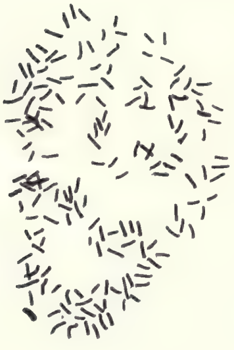
Figs 54a, b *Dryopteris viridescens, CRFJ* 9934: photograph and drawing of root tip mitosis showing *c.* 164 chromosomes.



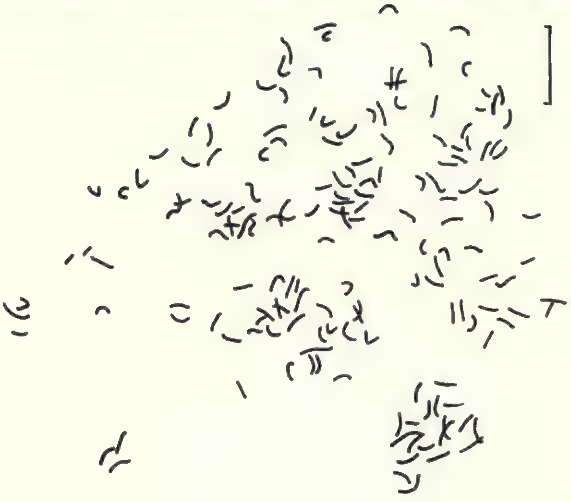
55a



56a



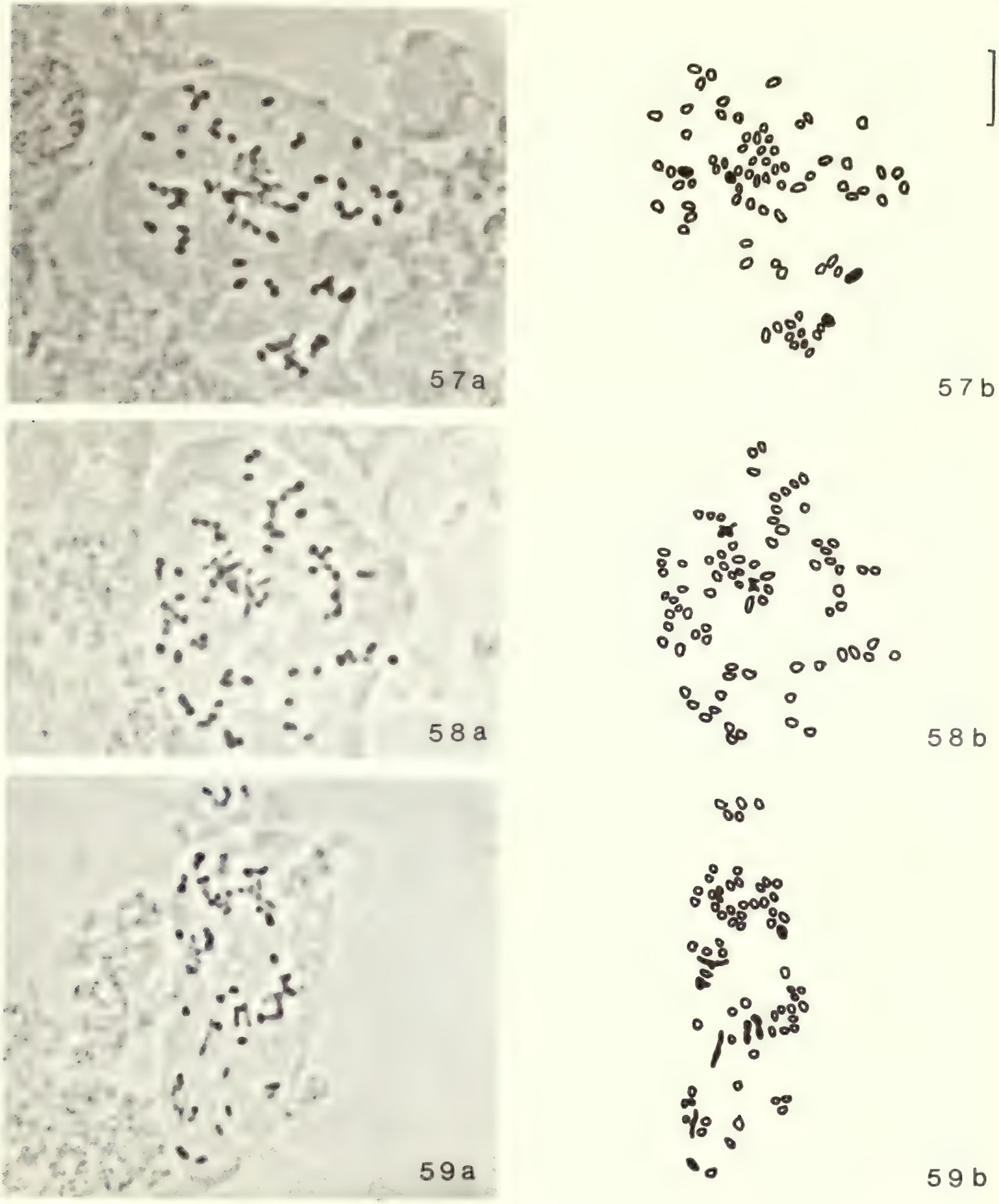
55b



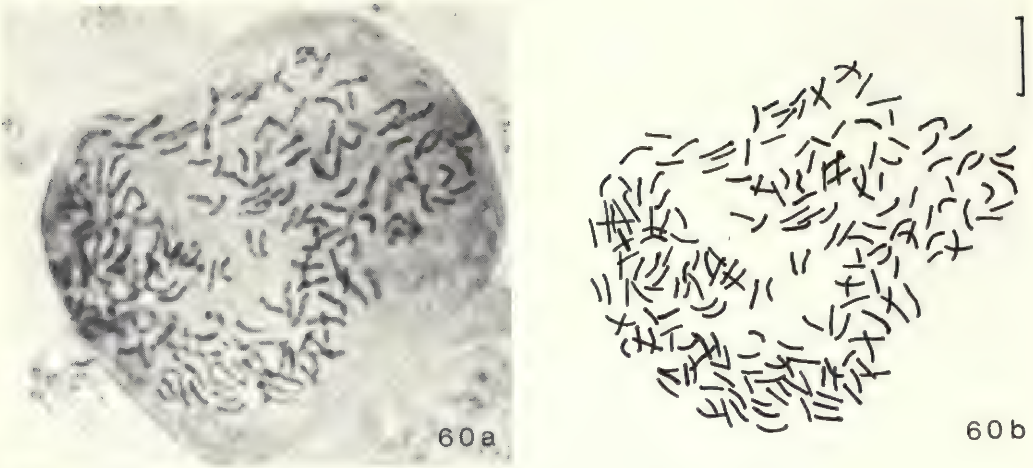
56b

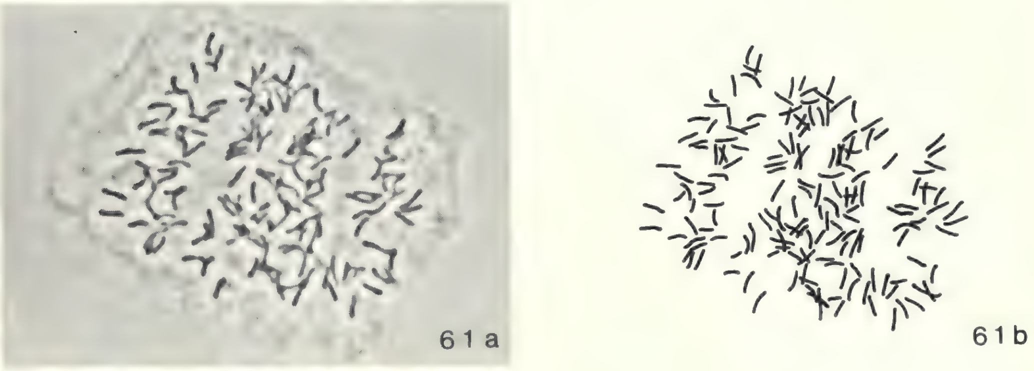
Figs 55a, b *Dryopteris viridescens, CRFJ* 10068: photograph and drawing of root tip mitosis showing 164 chromosomes.

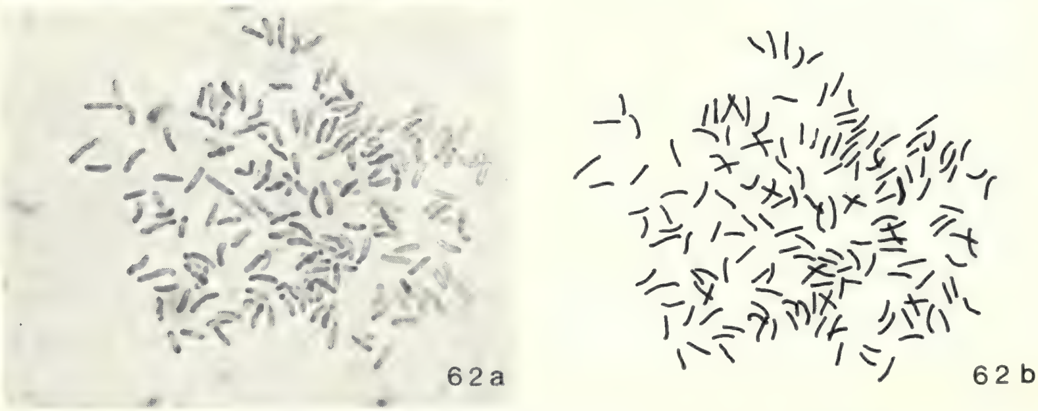
Figs 56a, b *Dryopteris* × *flemingii, CRFJ* 6968: photograph and drawing of root tip mitosis showing 164 chromosomes.



Figs 57–59 *Dryopteris* × *wechteriana, CRFJ* 6948: photograph and drawing of meiosis showing: 57a, b: 4 bivalents (in black) and 74 univalents (outlined); 58a, b: 2 bivalents (in black) and 78 univalents (outlined); 59a, b: 8 bivalents (in black) and 66 univalents.



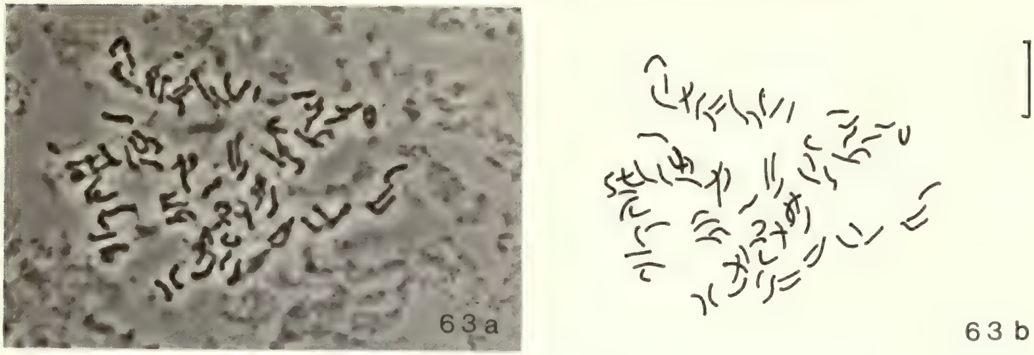


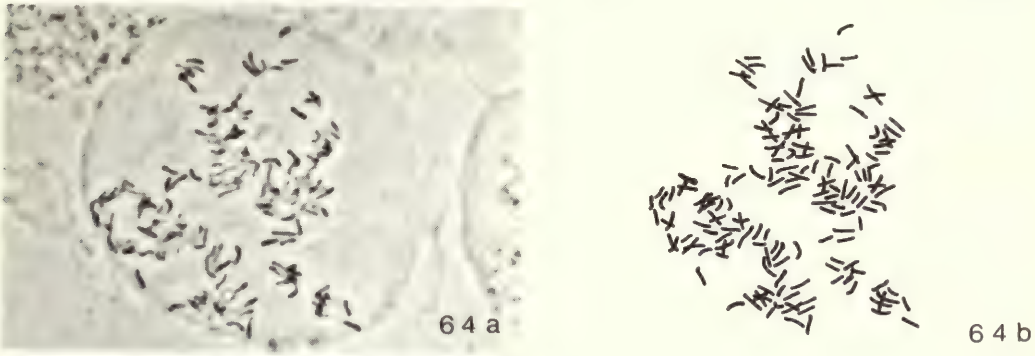


Figs 60a, b *Dryopteris × zygo-parentalis, CRFJ* 8577: photograph and drawing of root tip mitosis showing *c.* 200 chromosomes.

Figs 61a, b *Polystichum acutidens, CRFJ* 9945: photograph and drawing of root tip mitosis showing *c.* 164 chromosomes.

Figs 62a, b *Polystichum acutidens, CRFJ* 9947: photograph and drawing of root tip mitosis showing 164 chromosomes.


63 a
63 b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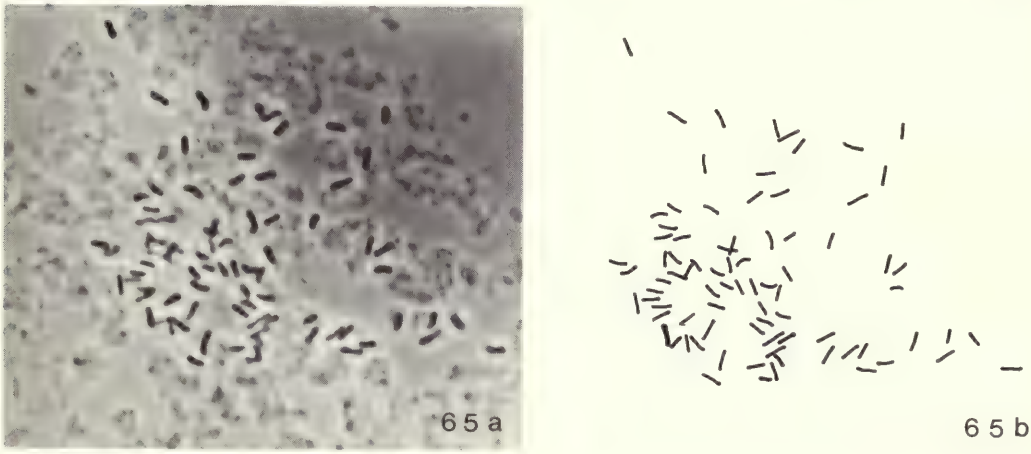
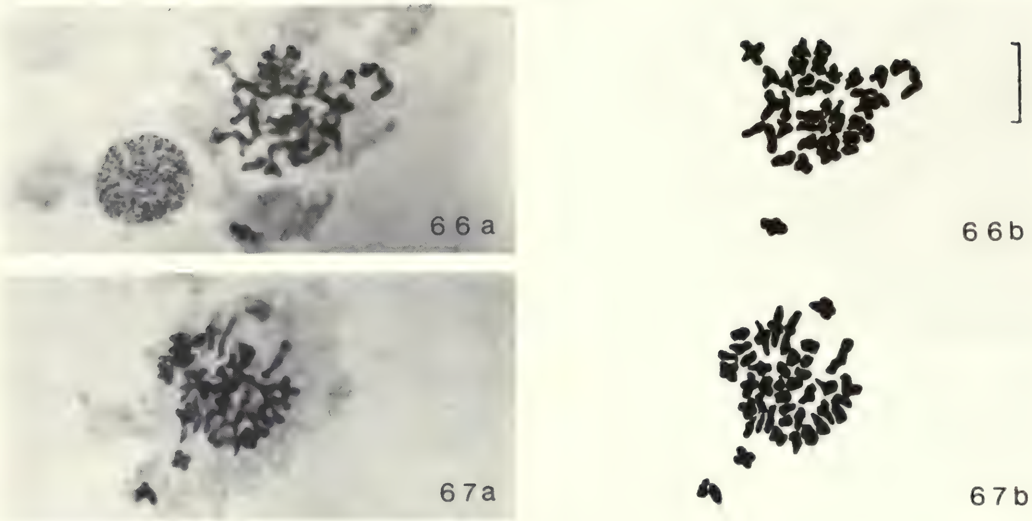
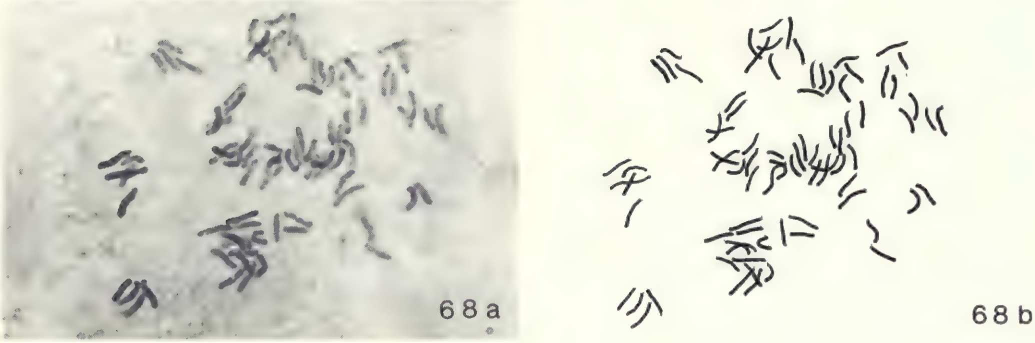

65 a
65 b

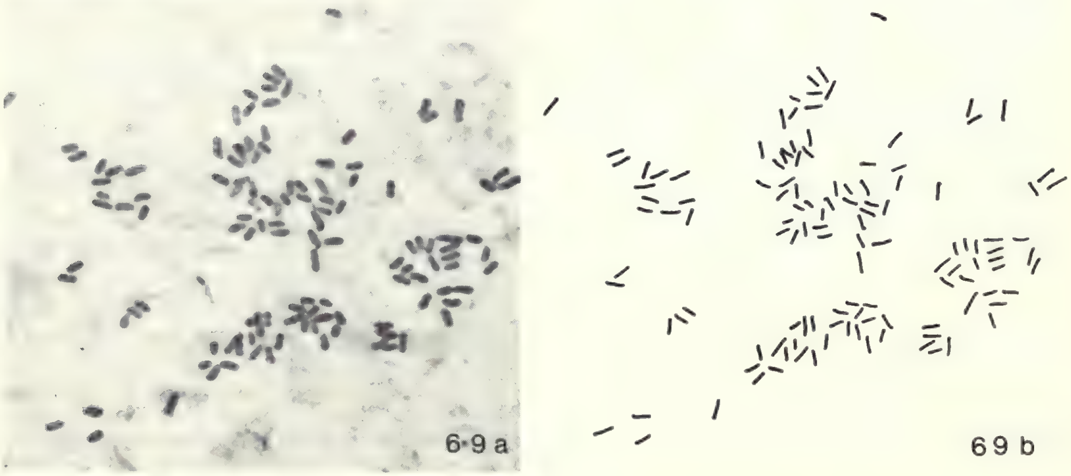
Figs 63a, b *Polystichum discretum, CRFJ* 6689: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 64a, b *Polystichum piceo-paleaceum, CRFJ* 7179: photograph and drawing of root tip mitosis showing 164 chromosomes.

Figs 65a, b *Polystichum lentum, CRFJ* 7153: photograph and drawing of root tip mitosis showing 82 chromosomes.



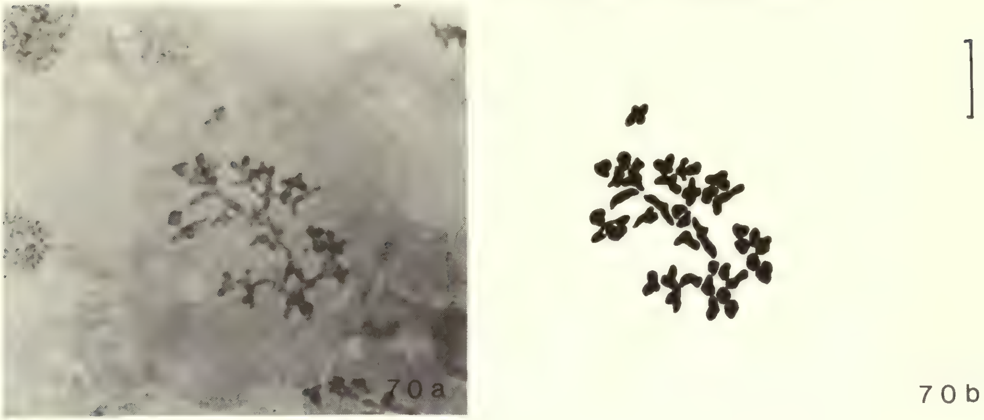


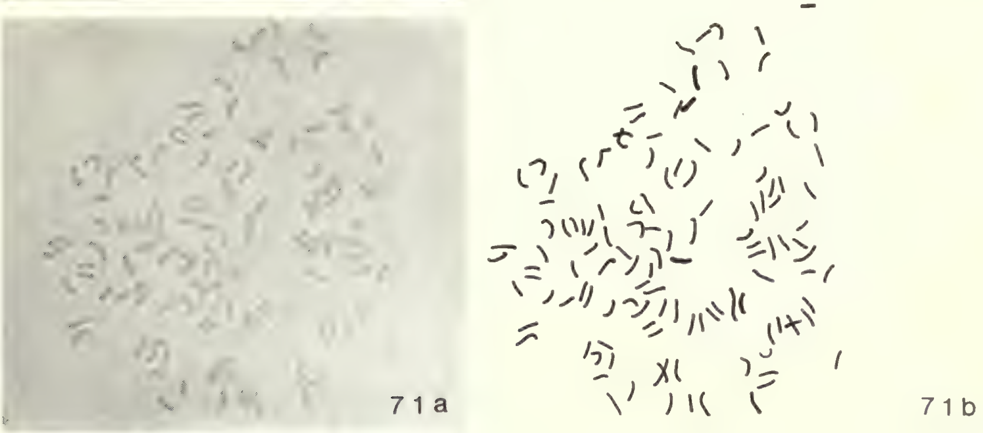


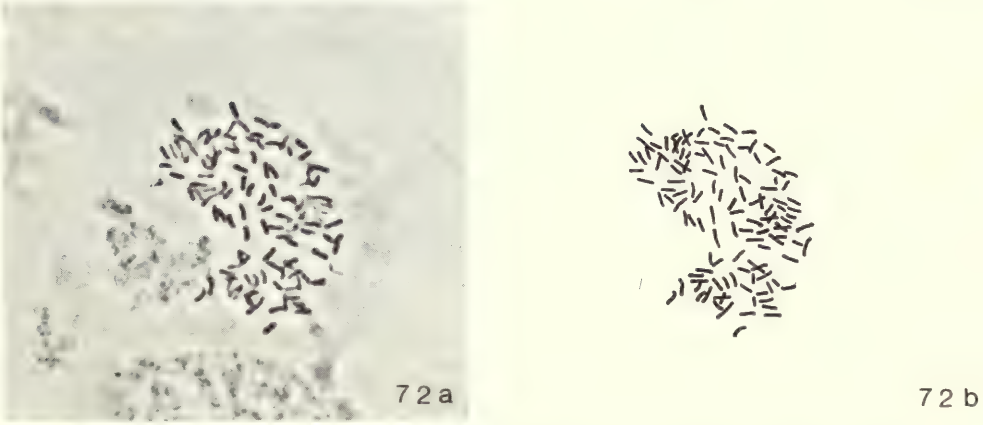
Figs 66a, b; 67a, b *Polystichum lentum, CRFJ* 7155: photograph and drawing of meiosis showing 41 bivalents (in black).

Figs 68a, b *? Polystichum pseudo-makinoi, CRFJ* 9929: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 69a, b *Polystichum xiphophyllum, CRFJ* 9921: photograph and drawing of root tip mitosis showing 123 chromosomes.



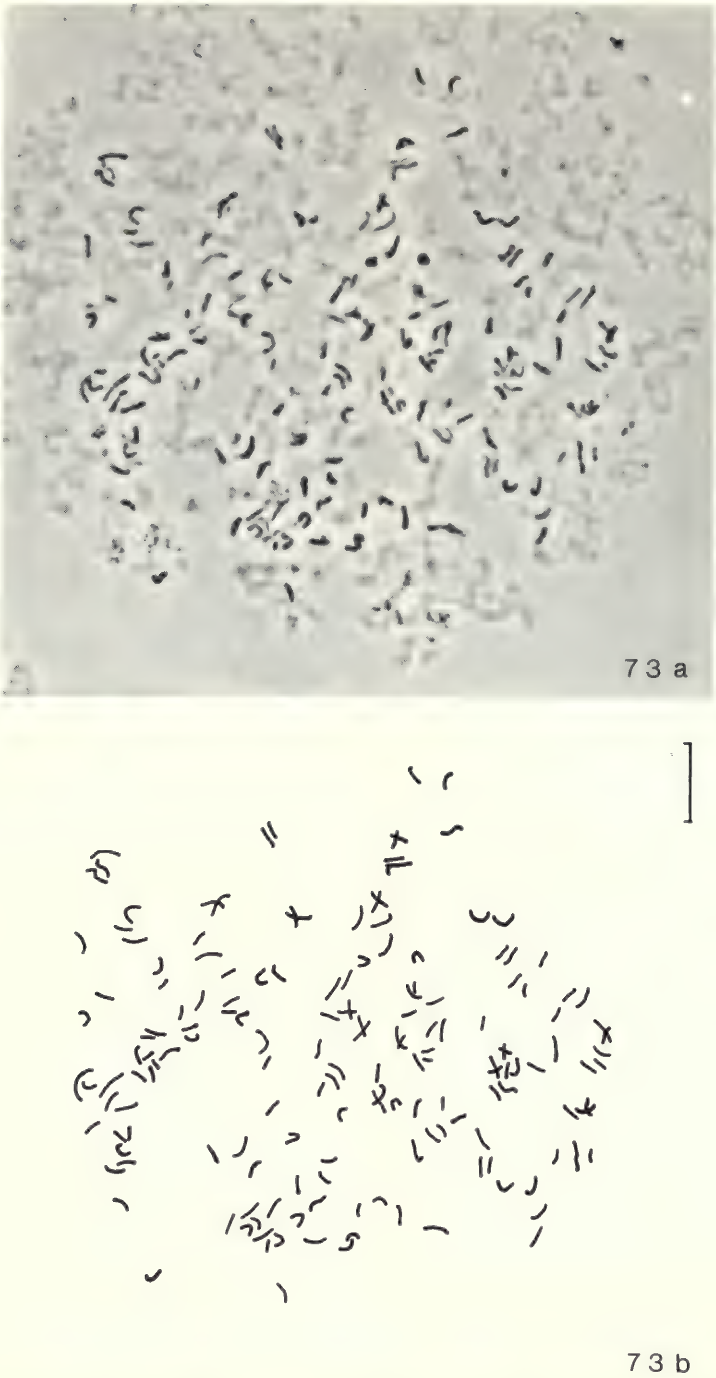




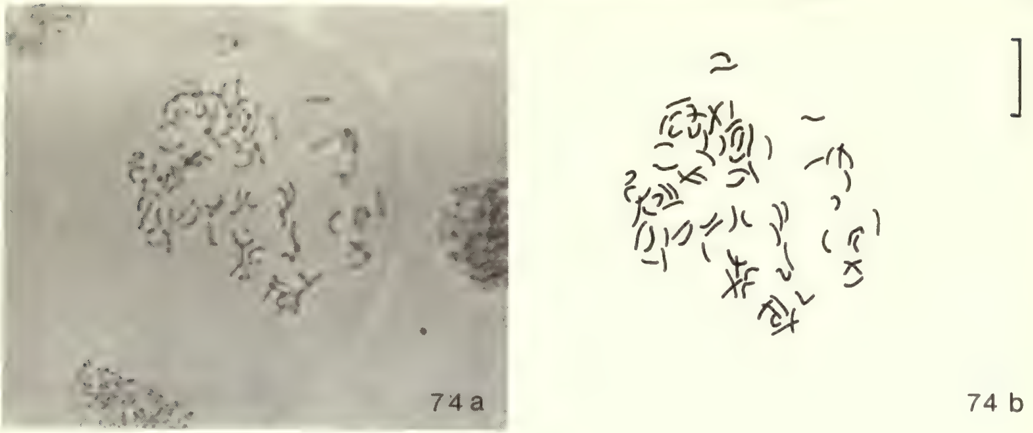
Figs 70a, b *Polystichum nepalense, CRFJ* 6792: photograph and drawing of meiosis showing 41 bivalents (in black).

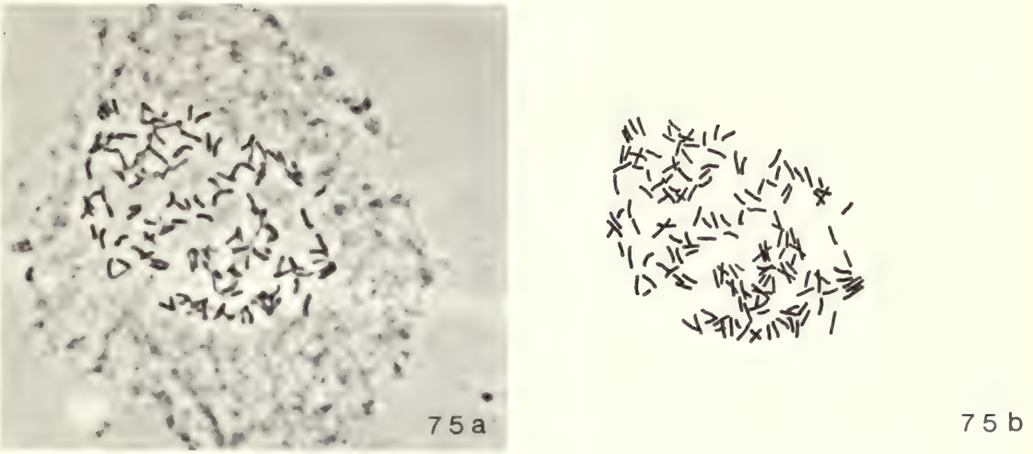
Figs 71a, b *Polystichum tsus-simense, CRFJ* 9940: photograph and drawing of root tip mitosis showing 123 chromosomes.

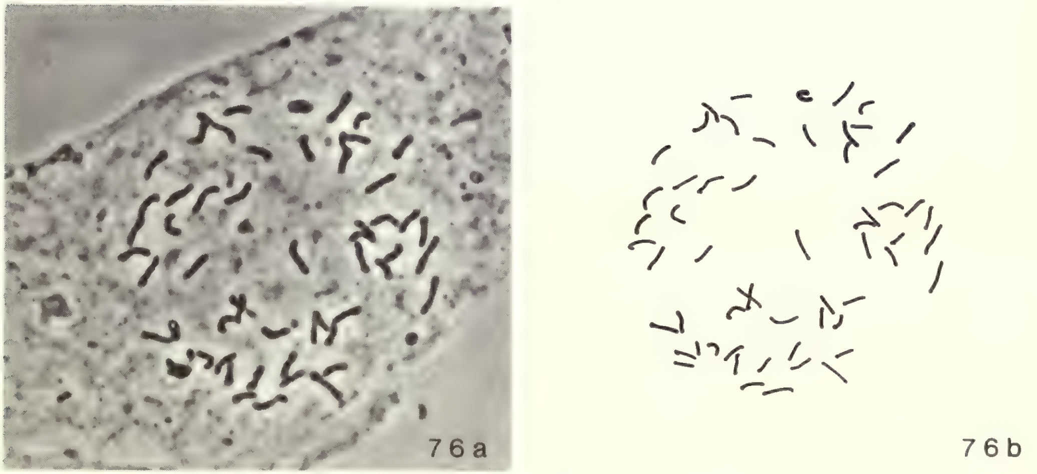
Figs 72a, b *Polystichum tsus-simense, CRFJ* 9999: photograph and drawing of root tip mitosis showing 123 chromosomes.



Figs 73a, b *Polystichum yunnanense, CRFJ* 9998: photograph and drawing of root tip mitosis showing 164 chromosomes.



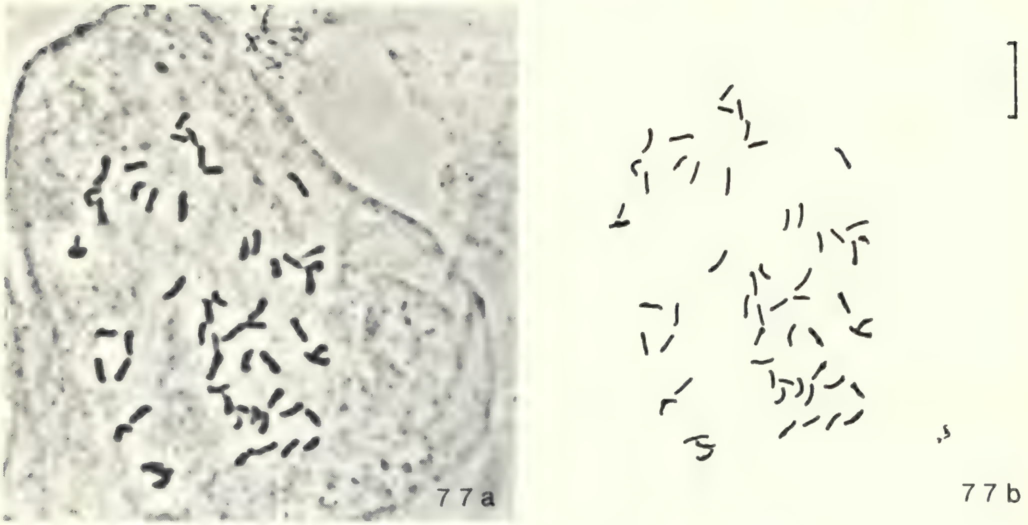


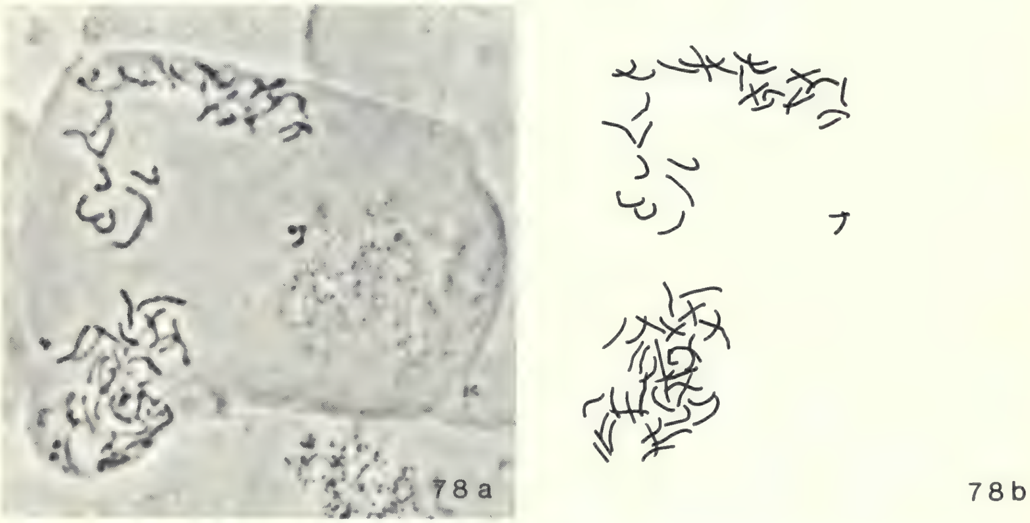


Figs 74a, b *Ctenitis mariformis, CRFJ* 9870: photograph and drawing of root tip mitosis showing 82 chromosomes.

Figs 75a, b *Hypodematium crenatum* agg., *CRFJ* 10015: photograph and drawing of root tip mitosis showing 164 chromosomes.

Figs 76a, b *Aleuritopteris albo-marginata, CRFJ* 6959: photograph and drawing of root tip mitosis showing 58 chromosomes.





Figs 77a, b *Aleuritopteris albo-marginata, CRFJ* 6959: photograph and drawing of root tip mitosis showing 58 chromosomes.

Figs 78a, b *Neocheiropteris palmato-pedata, CRFJ* 10017: photograph and drawing of root tip mitosis showing *c.*70 chromosomes.

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David L. Hawksworth

Botany series Vol 14 No 2 19 December 1985

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Contents

Synopsis 43
Introduction 44
History of usage 44
Material and methods 47
  Material 47
  Methods 47
Generic concepts 47
  Taxonomy 47
  Key to the genera 50
  Generic names 52
Species concepts 62
  Taxonomy 62
  Biological concepts 64
I. *Mycomicrothelia* 64
  Key to the species 65
  The species 67
II. *Peridiothelia* 120
  Key to the species 121
  The species 121
Excluded species 130
Acknowledgements 174
References 174
Index 177

Synopsis

Following a discussion of the usage of the name *Microthelia* Körber, generic concepts to be applied to the lichen-forming and non-lichenized species referred to it are reviewed. A key to 15 genera is provided and notes on 35 of the generic names used for bitunicate pyrenomycetes with brown 1-septate ascospores are presented. Detailed treatments are provided for the genera *Mycomicrothelia* Keissler (Arthopyreniaceae; 26 species) and *Peridiothelia* D. Hawksw. gen. nov. (Phaeosphaeriaceae; 3 species).

Two new species of *Mycomicrothelia* (*M. atlantica* D. Hawksw. & Coppins, *M. confusa* D. Hawksw.) are described and the following new combinations made: *M. anonacea* (Müll. Arg.), *M. apposita* (Nyl.), *M. captiosa* (Krempelh.), *M. confluens* (Müll. Arg.), *M. conothelena* (Nyl.), *M. dothideaspora* (Cooke & Harkn.), *M. fumulosa* (Zahlbr.), *M. miculiformis* (Nyl. ex Müll. Arg.), *M. minutula* (Zahlbr.), *M. modesta* (Müll. Arg.), *M. nonensis* (Stirton), *M. obovata* (Stirton), *M. pachnea* (Körber), *M. socialis* (Zahlbr.), *M. subfallens* (Müll. Arg.), *M. thelena* (Ach.), and *M. willeyana* (Müll. Arg.) D. Hawksw. combs nov. The predominantly tropical genus includes a mixture of doubtfully or facultatively lichenized and non-lichenized species; the latter are mostly host-specific. *Peridiothelia* includes three non-lichenized European species: *P. fuliguncta* (Norman), *P. grandiuscula* (Anzi), and *P. oleae* (Körber) D. Hawksw. combs nov.

The identities of 144 epithets described in or referred to *Microthelia* are reviewed as excluded species and the following new taxa introduced: *Arthopyrenia clavaeformis* (Stirton), *A. subgregans* (Müll. Arg.), *Didymosphaeria calyciospora* (Massal.), *Massarina ribesiella* (Nyl. ex Vainio), *Melanomma oxysporum* (Zahlbr.), *Muellerella vesicularia* (Lindsay), *Pleurotrema uniserialis* (Zahlbr.), *Polycoccum cartilaginosum* (Arnold), *P. innatum* (Müll. Arg.), *P. umbilicariae* (Lindsay), *P. vermicularium* (Lindsay), *P. versisporum* (Bagl. & Car.), *Polypyrenula* gen. nov. (Pyrenulaceae), *P. sexlocularis* (Müll. Arg.) D.

Bull. Br. Mus. nat. Hist. (Bot.) **14** (2): 43–181 Issued 19 December 1985

Hawksw. combs nov. Descriptions and illustrations (photographs and spore outlines) are provided for all accepted species of *Mycomicrothelia* and *Peridiothelia* and also of many of the taxa referred to other genera.

This paper concludes the first phase of a re-investigation of all bitunicate pyrenomycetes with paraphysate ascomata and brown one-septate ascospores.

Introduction

The systematics of the fissitunicate paraphysate pyrenomycetes with brown 1-septate ascospores has been badly neglecged in recent decades, with the result that taxa continue to be referred to entities based on outdated generic concepts, not indicative of either their systematic relationships or biology. With perhaps about 70 generic names and in excess of 1000 species epithets already in the literature this neglect is understandable, but unless inroads into this morass of names are made the existing confusions can only be compounded. This contribution aims to make some progress in improving this situation by providing a revision of all the taxa referred to a particular generic name in the group, *Microthelia* Körber. This name was selected as preliminary studies showed that it had come to be used in a variety of senses, even by contemporary authors, and was becoming a repository for a bewildering array of both lichen-forming and non-lichenized fungi. A critical study of these taxa also necessitates a re-appraisal of the criteria used for the separation of genera and species; this should prove of value, through extrapolation, in allied groups.

It would have been ideal to treat all taxa referred to *Didymosphaeria* Fuckel at the same time as those placed in *Microthelia*, but so many names are involved that the task could not be completed for many years. However, some epithets in *Didymosphaeria* may be expected to belong to genera or even species accepted in the present revision, rather than to *Didymosphaeria* itself (see p. 54). This paper can consequently also be viewed as a first contribution to a re-appraisal of taxa referred to *Didymosphaeria*. Further, epithets placed under both these generic names by different authors are considered.

There has been a tendency for students of pleosporaceous fungi to develop broad generic concepts in the temperate zone and then later attempt to accommodate tropical taxa within their limits. This approach has already led to considerable difficulties in some groups, for example the *Leptosphaeria*- and *Pleospora*-like fungi. The approach adopted here, a re-appraisal of the described world species prior to the formulation of generic concepts, should tend to reduce the risk of a similar situation arising in the *Didymosphaeria*- and *Microthelia*-like taxa, although the under-collecting of both lichen-forming and non-lichenized pyrenomycetes in the tropics means that the danger cannot be eliminated.

The number of epithets which have been referred to *Microthelia* or genera which have been considered as synonyms of it is 200. I have presented the results of my studies of three 'segregates' elsewhere, as they proved to be remote from the bulk of the taxa referred to *Microthelia*. These are *Astrosphaeriella* (Hawksworth, 1981*a*), *Kirschsteiniothelia* (Hawksworth, 1985*a*), and *Lichenothelia* (Hawksworth, 1981*b*). This paper is primarily concerned with general aspects of the group, the genera *Mycomicrothelia* and *Peridiothelia*, and the 144 names used in or referred to *Microthelia* which belong elsewhere. These names are treated in the section on excluded species, which also indexes relevant epithets discussed in Hawksworth (1981*a*, 1981*b*, 1985*a*).

History of usage

The generic name *Microthelia* (Gk μιχϱός, *micro* – small; ϑηλή, *thele* – wart or nipple) was first introduced by Körber (1855: 372) to accommodate perithecial taxa producing brown one-septate ascospores. He included four species in the genus, *M. micula* Flotow ex Körber, *M. atomaria* (Ach.) Körber, *M. propinqua* Körber, and *M. pygmaea* (Körber) Körber. The typification and nomenclature of these is considered under 'Excluded species' in this treatment but it is pertinent to mention their identities here: (1) *M. micula* = *Anisomeridium biforme* (Borrer) R. C. Harris (see p. 157), *M. atomaria* = *Leptorhaphis atomaria* (Ach.) Szat. (p. 135),

(3) *M. propinqua* = *Endococcus propinquus* (Körber) D. Hawksw. (p. 160), and (4) *M. pygmaea* = *Muellerella pygmaea* (Körber) D. Hawksw. (p. 160). The principal objective of Körber in introducing the name *Microthelia* appears to have been to replace *Tichothecium* Flotow (see p. 59), which he considered too similar to the name of the hyphomycete genus *Trichothecium* Link (Link, 1809: 18); as the type species of Flotow's name is *T. nigrescens* (Pers.) Flotow (i.e. *Verrucaria nigrescens* Pers.; see Hawksworth, 1979*a*) this interpretation renders *Microthelia* an obligate later synonym of *Verrucaria* Schrader nom. cons. Unfortunately the nomenclatural position here is complicated by Körber (1855: 341) having retained *V. nigrescens* in *Verrucaria* as a synonym of *V. fuscoatra* (Wallr.) Körber.

However, most authors since Fries (1861: 111) have unquestioningly cited *M. micula* as the type species of Körber's generic name, misapplying it to the taxon named as *Peridiothelia fuliguncta* (Norman) D. Hawksw. in this revision, and not appreciating that the epithet *micula* was intended as a replacement for Borrer's '*biformis*' (see p. 157). Harris (1973: 26) first pointed out that '*micula*' could be treated as superfluous but retained both genus and species names as an interim measure. To select *M. propinqua* or *M. pygmaea* could threaten *Endococcus* Nyl. or *Muellerella* Hepp ex Müll. Arg. respectively. The nomenclatural situation was considered further by Hawksworth & Sherwood (1981: 339–340) who concluded that it was most appropriate to use the conservation procedures and proposed *Anisomeridium* (Müll. Arg.) M. Choisy for conservation over *Microthelia*, with *M. micula* nom. illegit. as the lectotype of the later name. Whatever the outcome of this proposal, Körber's name will continue to be unavailable for any of the genera recognized in this present revision.

The heterogeneity of Körber's concept of *Microthelia* was quickly recognized by his contemporaries. Massalongo (1856: 57–8) restricted the genus to three species which he considered (incorrectly) to be lichenized: '*M. biformis*', *M. atomaria*, and the newly described *M. macularis* Hampe ex Massal. (i.e. *Mycomicrothelia macularis* (Hampe ex Massal.) Keissler; p. 92), referring the lichenicolous species to *Tichothecium*. The name was not accepted by Nylander (1858: 60) in his synopsis of the pyrenocarpous lichens, *M. micula* being placed as synonym of *Verrucaria cinerella* Flotow (i.e. *Mycomicrothelia melanospora* (Hepp) D. Hawksw.; p. 95). Trevisan (1860: 10) attributed the genus to 'Körb. (exclus. spec. parasit. – 1856)' following Massalongo, and excluding the lichenicolous taxa. Trevisan accepted seven corticolous (including both *M. micula* and *M. atomaria*) and one saxicolous species.

Körber (1865: 396–399), however, maintained a broad concept of the genus admitting six species additional to his 1855 treatment; these included a wide range of fungi with ± perithecial ascomata and brown one-septate ascospores including lichen-forming, non-lichenized, and lichenicolous species. He harshly rejected Massalongo's (1856) interpretation, which he viewed as illogical in splitting species out on a biological basis.

A remarkable usage of *Microthelia* is seen in the works of Lindsay (e.g. 1869: 519) who provisionally adopted the name as a 'pseudo-genus' for a wide range of lichenicolous fungi 'confessedly most diverse in character'. Taxa with simple, 1-septate, or 3-septate, brown or colourless spores were included, drawn from a wide range of groups, even including some Coelomycetes.

Fuckel (1870: 140–142) introduced a new genus, *Didymosphaeria* Fuckel, for fungi occurring on lichens or phanerogams which recalled *Pleospora* but had brown one-septate ascospores. Rehm (1879) recognized that this posed problems and endeavoured to restrict *Didymosphaeria* to non-lichenized and *Microthelia* to lichen-forming species; six species were referred to the latter group, but none of these are now considered as definitely lichenized. Stein (1879: 331), however, had a different view separating *Tichothecium* from *Microthelia* on the basis of habitat, restricting the latter to species on bark. Niessl (1881) rejected Rehm's interpretation also, drawing attention to differences in ascomatal structure and comparing *Microthelia* to *Massariopsis* Niessl (i.e. *Amphisphaeria* Ces. & de Not.; see Müller & von Arx, 1973: 120). However, a more superficial view was adopted by Saccardo (1882: 709) who treated *Microthelia* as a synonym of *Didymosphaeria*.

The first author to endeavour to deal with tropical *Microthelia*-like taxa in detail was Müller Argoviensis (1885: 416–7). He recognized two groups in material from Cuba he attributed to the genus, one with 'Perithecia dimidiata' and the other 'Perithecia globosa aut subglobosa'. Later he extended the concept of the genus to include a species with (3–)5 septate spores, *M. sexlocularis* Müll. Arg. (Müller Argoviensis, 1888: 38); Clements (1909: 173) placed the latter in a new monotypic genus, *Polythelis* Clem. (see p. 165).

Jatta (1911), in providing a treatment of the Italian species, recognized four sections in the genus based on the numbers of spores in the asci and whether the cells in the spores were equal or unequal in size. Vainio (1921*a*), however, formally recognized the two groups of Müller Argoviensis (1885), and introduced the sectional name *Holothelia* Vainio for that with entire ascomata and *Hemithelia* Vainio for the one with dimidiate ascomata.

In his careful re-evaluation of the Finnish lichenized pyrenomycetes, Vainio (1921*b*: 144) used '*Microthelia* (Koerb.) Vain.' for the single lichenized maritime species *M. scopularia* (Nyl.) Blomb. & Forss., though noting that *M. metzleri* Lahm was also close to this species. In character with his treatment of other groups, Vainio did not retain non-lichenized species in a genus he interpreted as lichenized. Thus, he took up *Didymosphaeria* Fuckel for the consistently non-lichenized corticolous species ('*D. micula* (Flotow) Vainio', *D. analeptoides* (Bagl. & Car.) Vainio, *D. ribesiella* (Nyl.) Vainio, *D. wallrothii* (Hepp) Sacc. & Trott., and a few non-Finnish species treated cursorily). This interpretation was rejected by Zahlbruckner (1926*a*: 75), however, who continued to follow a broad concept of the genus – at the same time misinterpreting Vainio's sectional names.

Keissler (1936: 21–57) utilized Vainio's sectional classification and, in the first attempt at a critical re-appraisal of the central European species, recognized eight species in the genus, viz. '*M. micula*' (with f. *grandiuscula* (Anzi) Keissler), *M. pachnea* Körber, '*M. atomaria*' (with f. *calyciospora* (Massal.) Keissler), *M. macularis* Massal. (with f. *ribesiella* (Nyl.) Keissler), *M. oleae* Körber, *M. betulina* Lahm, *M. aterrima* (Anzi) Zahlbr. (with f. *atramentea* (Norman) Keissler, var. *dermatinoides* Servít), and *M. marmorata* Hepp ex Körber (with f. *cartilaginosa* (Arnold) Keissler, f. *minor* (Kernst.) Keissler). Keissler simultaneously proposed the new genus *Mycomicrothelia* Keissler for two non-lichenized species with dimidiate ascomata accepted in his treatment, '*M. atomaria*' and *M. macularis*. In introducing this generic name he separated it from *Didymosphaeria* on the basis of the dimidiate rather than entire ascomata. In addition, Keissler provided notes on the identities of 38 excluded or imperfectly known species, the types of some of which he had studied.

The next significant contribution to our knowledge of the *Didymosphaeria*-like fungi was that of Scheinpflug (1958) who recognized four groups within the genus. He did not discuss *Microthelia* itself, but placed *M. micula* as a synonym of a species he referred to as *Astrophaeriella pinicola* (Rehm) Scheinpflug (i.e. *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw.; see p. 50, Hawksworth, 1985*a*)). Müller & von Arx (1962: 282–284) realized that this situation was not satisfactory, and re-instated *Microthelia*, placing *Astrosphaeriella* Sydow & H. Sydow, *Jahnula* Kirschst., and *Kirschsteiniella* Petrak as synonyms. *Didymosphaeria* was used for species with entire ascomata, *Microthelia* for ones which were hemispherical and superficial, while *Mycomicrothelia* was employed for immersed dimidiate ascomata. While this was the first time that the justification of separating Keissler's genus *Mycomicrothelia* on structural rather than biological grounds had been appreciated, the broad view of *Microthelia* adopted placed together a disparate assemblage of six species (five newly combined into the genus) which subsequent more detailed studies have shown must be dispersed between four genera referred to different families of Dothideales.

Poelt (1969: 394–397) did not follow Müller & von Arx (1962) but retained Keissler's (1936) broad concept of the genus. He provided keys to 13 species accepted as occurring in central Europe, arranged according to Vainio's subgenera. The importance of the reaction of the centrum with iodine in separating the dimidiate taxa was stressed, and species groups broadly equivalent to *Peridiothelia* and *Mycomicrothelia* as accepted in this revision were distinguished. Subsequently those working with lichens have tended to follow Poelt (e.g. Harris, 1973), while other mycologists have adhered to the schemes of either Scheinpflug (e.g. Dennis, 1968), or Müller & von Arx (e.g. Kohlmeyer & Kohlmeyer, 1979: 429–431).

It is also pertinent to draw attention here to the use of *Microthelia* for the teleomorph (perfect state) of the dematiaceous hyphomycete *Dendryphiopsis atra* (Corda) S. Hughes by Corlett & Hughes (Hughes, 1978: 360–362); this fungus is now referred to *Kirschsteiniothelia* (Hawksworth, 1985*a*).

In order to clarify this confused situation my own investigations on the taxa referred to *Microthelia* were initiated in 1979 (Hawksworth, 1981*a*, 1981*b*, 1984, 1985*a*; Hawksworth & Sherwood, 1981). The present contribution completes this first phase of my investigations on the *Didymosphaeria*-like fungi.

Material and methods

Material

In the course of this study, collections have been received on loan or studied in the following institutional herbaria: BG, BM, CAN(L), DAOM, E, G, H, IMI, K, L, LPS, M, NY, O, PAD, PC, S, TNS, TRH, TUR, UPS, VER, W, WELT, WRSL, and ZT (abbreviations follow Holmgren et al., 1981), and the private herbarium including H. Fabre's material at L'Harmas.

Methods

Macroscopic features were studied with a Nikon stereomicroscope fitted with a measuring eyepiece graticule and zoom lens (to × 60). Microscopic characters were investigated with an Olympus BH or BH-2 microscope equipped with Nomarski Differential Interference Contrast (DIC) optics, a drawing tube, and camera. Magnifications up to × 1562 were used for measurement with an eyepiece graticule, and drawings were routinely made at × 3300. Macroscopic photographs were taken on a Zeiss Tessovar system with zoom lenses, and those of sections and microscopic features in the Olympus microscopes used.

For each specimen 1–2 of the larger ascomata were removed and vertical sections cut at a thickness of 10 μm with an LBH freezing microtome. These sections were mounted in lactophenol-cotton blue (LCB), warmed, and sealed with Glyceel when cold for the examination of ascomatal structre; most sections preserved in the course of this study have been preserved in IMI. In addition ascomata were cut open with the aid of a surgical scalpel blade, and rough hand-cut sections mounted in 10% potassium hydroxide or Lugol's iodine solution. Where no reaction with Lugol's solution was obtained, specimens were pre-treated with potassium hydroxide and a mount also made in Melzer's iodine solution to check negatives. Measurements of ascospores were made on spores not included within asci (although many of these would have been released in the mounting process). Wherever the material permitted, at least 10 ascospores were measured and drawn using the drawing tube fitted to the microscope. Where pycnidia were being investigated, erythrosin in ammonia was used as a mountant to show details of the conidiogenous cells.

Scanning electron micrographs were taken on the ISI-60 SEM at CMI using air-dried specimens mounted on stubs with double-sided Sellotape and coated with gold.

Generic concepts

Taxonomy

As will be evident from the above review of the history of the usage of the name of *Microthelia* (pp. 44–47), generic concepts in the fungi to which this name has been applied have not previously been critically revised. Features such as ascospore colour and septation which had been stressed as generic criteria by most mycologists and lichenologists in the period 1880–1940 led to heterogeneous assemblages of often rather distantly related species being included under a single generic name (e.g. *Karschia* Körber, see Hafellner, 1979), and closely related species being dispersed amongst several generic names (e.g. *Micarea* Fr., see Coppins, 1983). The situation in *Microthelia* was found to be similar to that formerly existing in *Karschia*, but is probably not atypical of most pyrenocarpous genera, including lichen-forming species which are predominantly tropical.

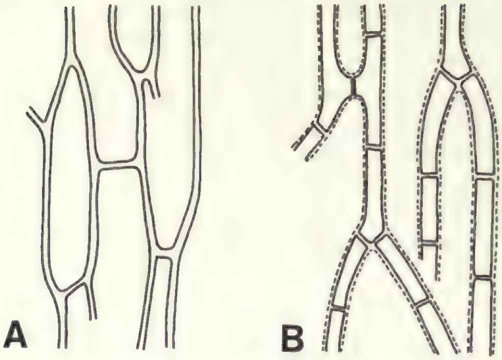

Fig. 1 **A**, Paraphysoids (trabeculate pseudoparaphyses). **B**, Pseudoparaphyses (cellular pseudoparaphyses).

The ontogeny of the ascoma and structure of the ascus are now generally accepted as of principal importance in the classification of the Ascomycotina (Hawksworth, 1985*b*). In the case of the main genera accepted in this revision, the ascus structure is typically bitunicate and discharge almost certainly fissitunicate. However, there is considerable variation in the structure of ascomata produced, and it is this character which proves to be of major importance for the recognition of genera here.

The nature of the interascal tissue, or rather 'hamathecium' (Eriksson, 1981), present in the ascomata is related to its ontogeny. In one group of species this was found to consist of paraphysoids (trabeculate pseudoparaphyses) attached at the top and base of the ascomatal cavity; these are produced by a stretching of the former interascal cells as the ascomata mature and finally appear only 1–1·5 μm thick, very rarely septate, and delicately branched and anastomosed (Figs 1a, 4c). The species with this type of hamathecium had carbonaceous ascomatal walls, often almost hyaline, and in several species multiseptate ascospores; all occurred on palms, bamboos or other stout grasses in the tropics and are non-lichenized. This assemblage of species is referred to *Astrosphaeriella* Sydow & H. Sydow (Hawksworth, 1981*a*; Figs 2a, 4). *Astrosphaeriella* belongs to the family Melanommataceae Winter, placed in the Melanommatales by Barr (1979*a*) and the Dothideales by Eriksson (1982).

The ontogeny of the main saxicolous group of species referred to *Microthelia* was found to be most distinctive by Henssen & Jahns (1973: 113 fig. 4.18 k–m) in that the ascomata are disc-like and superficial from a very early stage (Fig. 6B) with the asci finally arranged almost palisade-like in a hymenium separated by paraphyses-like branching filaments firmly attached at the base (Fig. 2D). In the other main groups, discussed below, the asci remain enclosed in a perithecium-like ascoma. The two species recognized are also of interest in that they have ± smooth-walled ascospores with gelatinous sheaths swelling markedly in potassium hydroxide and spores which may become 3-septate; one has asci in which the outer wall turns blue in iodine (Fig. 6C), and they are biologically similar in forming a black superficial crustose 'thallus' but may be more appropriately regarded as algal parasites than as truly lichenized. The new generic name *Lichenothelia* D. Hawksw. was introduced for these species (Hawksworth, 1981*b*), the family placement of which within the Dothideales remains uncertain.

Mycomicrothelia is distinguished from the other two genera recognized with cellular pseudoparaphyses (Fig. 1B) and ascomata opening by a small circular ostiole by the development of the generative tissue beneath a clypeate involucrellum; this covering layer is made up of cells of the outer peridermal or epidermal layers intermixed and bound together by brown hyphae which form a strong covering tissue (Fig. 3C). In some cases the hyphae extend to form a conspicuous fringe extending beyond the involucrellum (e.g. *M. melanospora, M. wallrothii*; Fig. 2F), in which case the generative locule is often surrounded by a clearly differentiated thin exciple, while in others the hyphae are restricted to the area immediately surrounding the generative locule with no clearly differentiated exciple (e.g. *M. confusa, M. thelena*; Fig. 2G). For some

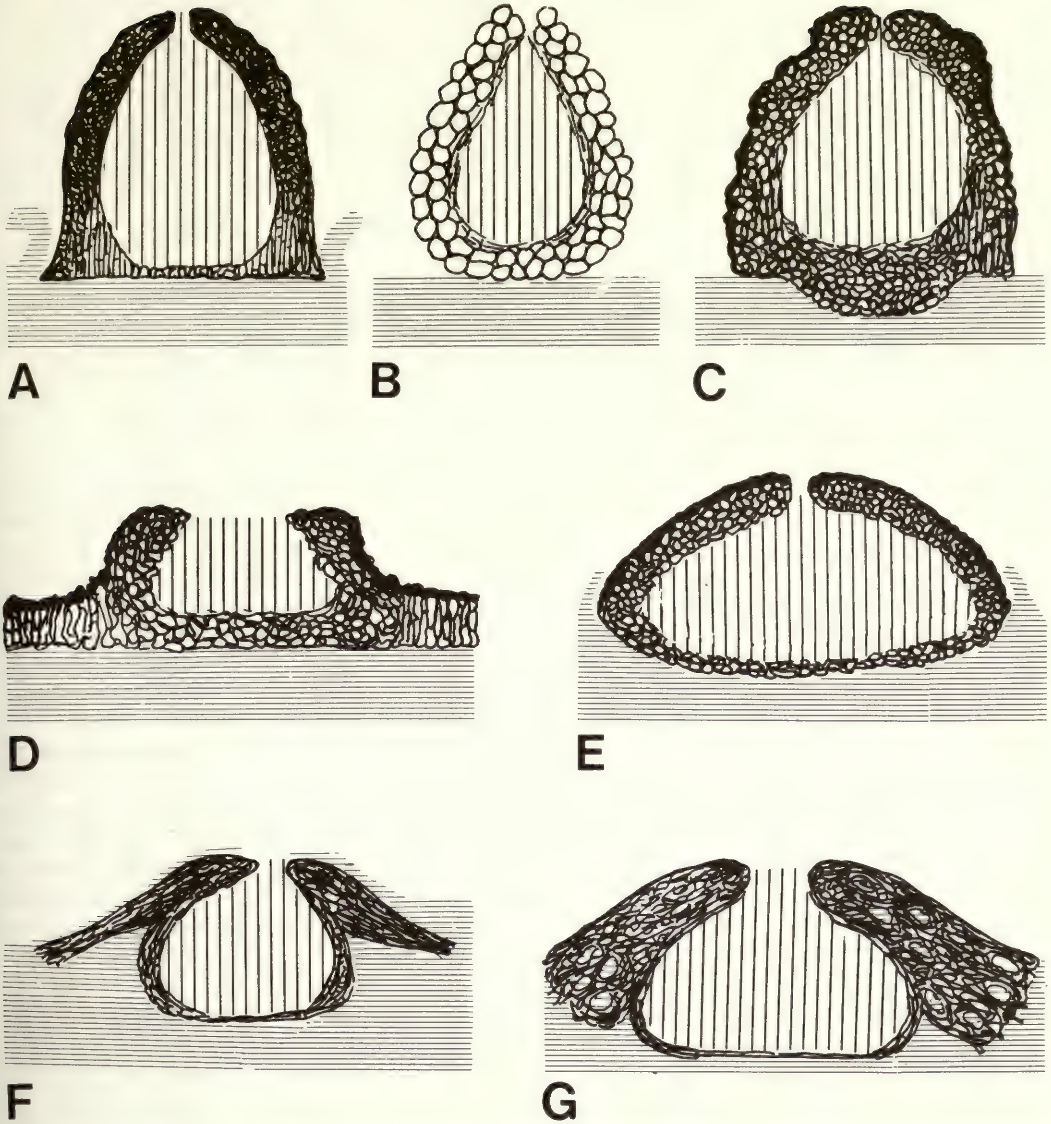

Fig. 2 Ascoma types of the principal genera included in the concept of *Microthelia* by previous authors (diagrammatic). **A**, *Astrosphaeriella*. **B**, *Jahnula*. **C**, *Kirschsteiniothelia*. **D**, *Lichenothelia*. **E**, *Peridiothelia*. **F**, *Mycomicrothelia* (*M. macularis* type). **G**, *Mycomicrothelia* (*M. thelena* type). Not to scale. Substratum and(or) host tissue indicated by horizontal parallel rules.

time I considered separating these two groups at the generic level but some species (e.g. *M. socialis*) are rather intermediate in structure and a broader generic concept is consequently more appropriate. The species grouped in this way are probably mainly non-lichenized and restricted to particular hosts, but some do seem to have trentepohlioid algae associated with them when fresh. This situation is strongly reminiscent of *Arthopyrenia* s.str. (Harris, 1975) and I endorse the view of Barr (1979*a*) that *Mycomicrothelia* should be referred to the family Arthopyreniaceae W. Watson. *Mycomicrothelia* is very close to *Arthopyrenia* s.str. and is distinguished from it only in that the ascospores become brown while still within the asci and have a verruculose ornamentation. This affinity is further supported by the dimidiate form of the ascomata in almost all species and also by the presence of pycnidia with bacillariform conidia in

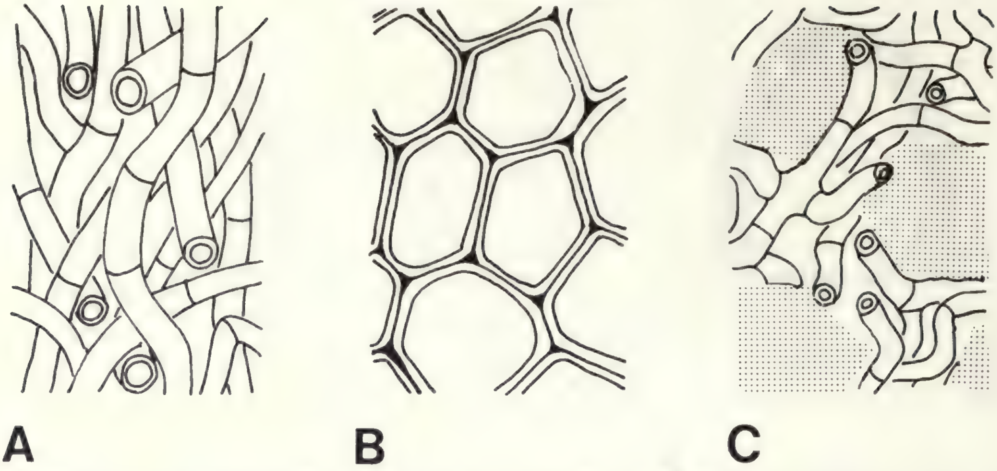

Fig. 3 Tissue types in ascoma walls. **A**, Hyphal (textura intricata). **B**, Cellular (pseudoparenchymatous; textura globulosa or textura angularis). **C**, Clypeate (host cells, dotted, bound together and interspersed by fungal hyphae).

several *Mycomicrothelia* species. Further, old ascospores within the ascomata of *Arthopyrenia* species may become brownish as they degenerate; it is not surprising therefore that some names included within *Microthelia* must be referred to *Arthopyrenia* (see 'Excluded species').

Kirschsteiniothelia (Figs 2C, 6A) and *Peridiothelia* (Fig. 2E) both differ from *Mycomicrothelia* in that the ascomata are erumpent and finally ± completely superficial. The ascomatal walls consist entirely of fungal tissue and do not have host cells as an integral part of their composition. In *Kirschsteiniothelia* the ascomatal wall is clearly pseudoparenchymatous with rather angular cells (Fig. 3B; textura angularis to textura prismatica) and a palisade of cells is often visible in the angles or at the base of the ascomata; in addition the ascomata become flattened at a late stage, the centrum is almost invariably unchanged with iodine, and the ascospores are often attenuated apically, with a thin gelatinous sheath. The six species accepted in this genus are essentially lignicolous saprophytes and where an anamorph is known this is a hyphomycete (Hawksworth, 1985*a*). In contrast, the ascomata of *Peridiothelia* have a wall consisting of small irregularly thickened rather rounded pseudoparenchymatous cells (textura globulosa), for the most part only becoming angular towards the base and especially in the angles of the ascomata (textura angularis); in addition the centrum tissues consistently turn blue in iodine and the ascospores have rounded apices and a conspicuous gelatinous sheath swelling in potassium hydroxide. Anamorphs are unknown in all the *Peridiothelia* species, which occur on the bark of living trees. *Kirschsteiniothelia* and *Peridiothelia* species do not appear to be lichen-forming. In the scheme of Barr (1979*a*), *Kirschsteiniothelia* would be referred to the family Pleosporaceae Nitschke as the ascomatal walls are ± equal in thickness or thickened at the sides but further on the basis of the hyphomycetous anamorph, and *Peridiothelia* to the Phaeosphaeriaceae Barr as the ascomatal walls are ± equal in thickness or thickened above and no hyphomycetous anamorph is known.

The main distinguishing features between the accepted genera are summarized in Table 1, and the differences in ascomatal structure are illustrated diagrammatically in Fig. 2.

Key to the genera

The following key includes the genera accepted in this revision (Table 1), together with other genera with 'bitunicate' asci and brown 1-septate ascospores which have been confused with these in the past. It is important to stress that this key does not purport to be a complete survey of genera with these characters. Many more taxa need to be studied before such a key can be produced. Further notes on the genera keyed out here are provided in the following section (pp. 52–62).

Table 1 Summary of characters separating the principal genera included within the concept of *Microthelia* by previous authors (see also Fig. 2).

	Astrosphaeriella	*Jahnula*	*Kirschsteiniothelia*	*Lichenothelia*	*Mycomicrothelia*	*Peridiothelia*
Family	Melanommataceae	Uncertain	Pleosporaceae	?Mycoporaceae	Arthopyreniaceae	Phaeosphaeriaceae
Ascoma						
Position	Erumpent or rarely immersed	Superficial	Superficial, immersed at base	Superficial, arising from 'thallus'	Immersed to somewhat erumpent	Erumpent, immersed at base
Shape	Conical, base flattened or ± dimidiate	Pyriform, base rounded and entire	Mammiform to pyriform, base often flattened but ± entire	Disc-like, base entire	Applanate, rarely mammiform, ± dimidiate	Mammiform, ± dimidiate but base usually continuous
Wall	Carbonaceous and cellular (textura angularis or prismatica)	Cellular (cells large; textura angularis)	Cellular (cells medium; textura angularis or prismatica)	Hyphal	Clypeate hyphal involucrellum, ± hyphal exciple (textura intricata)	Cellular (cells small; textura globulosa or angularis)
Colour (K[1])	Unchanged	Unchanged	Unchanged	Unchanged	Olivaceous	Unchanged
Hamathecium	Paraphysoids	?Paraphysoids	Pseudoparaphyses	Paraphysis-like pseudoparaphyses	Pseudoparaphyses	Pseudoparaphyses
Centrum (I[2])	Unchanged	Unchanged	Unchanged or rarely blue	Unchanged (or ascus sheath blue)	Unchanged or rarely violet	Blue
Ascospores						
Septa	1–6	1	1	1–3	1(–3)	1
Cells	Equal	Equal	± Equal	± Equal	Lower cell often smaller or ± equal	± Equal
Colour	Subhyaline, straw to red-brown	Brown (red-brown)	Brown (usually red-brown)	Brown (very dark)	Brown (usually olivaceous)	Brown (usually red-brown)
Sheath	Poorly developed	Poorly developed	Poorly developed	Well-developed and conspicuous	Moderately to well-developed	Poorly developed
Anamorph	Unknown	Unknown	Hyphomycetous where known (*Dendryphiopsis*)	Unknown	Coelomycetous where known	Unknown
Biology	Saprophytic or parasitic (esp. on palms and bamboos)	Saprophytic on wood (aquatic)	Saprophytic on wood (esp. conifers and deciduous trees)	Algicolous or lichenized on rock	Lichenized or saprophytic on bark	Saprophytic on bark (esp. deciduous trees)
Number of species	10	1	6	2	26	3

[1] 10% potassium hydroxide.

[2] Lugol's iodine.

1 Asci bitunicate in structure, lacking an apical ring turning blue with iodine, discharge fissitunicate 2
– Asci unitunicate in structure, with an apical ring turning blue with iodine, discharge not fissitunicate .... **Amphisphaeria** (p. 53)

2 (1) Ascomatal wall hyphal or of cells less than 20 μm diam 3
– Ascomatal wall with the outer layers composed of pseudoparenchymatous cells 20–30 μm diam; wall continuous below the centrum and ± even in thickness except in the immediate vicinity of the ostiole; superficial; on submerged wood, Europe ... **Jahnula** (p. 56)

3 (2) Interascal tissue (hamathecium) persistent 4
– Interascal tissue (hamathecium) absent 14

4 (3) Hamathecium composed of trabeculate pseudoparaphyses (paraphysoids), usually less than 1·5 μm thick; sometimes developing true paraphyaes later 5
– Hamathecium composed of cellular pseudoparaphyses, usually exceeding 1·5 μm thick 8

5 (4) Ascomata immersed, entire, the wall continuous and ± equal in thickness throughout 6
– Ascomata erumpent to superficial, dimidiate, the base not continous or much reduced in thickness; ascospores fusiform, 1-many septate, often rather pale; on palms and stems of bamboos or other stout grasses, tropical .... **Astrosphaeriella** (p. 53)

6 (5) Ascomatal walls dark-brown and pigmented throughout 7
– Ascomatal walls ± hyaline except in the vicinity of the ostiole where a thickened region develops .... **Didymosphaeria** (p. 54)

7 (6) Ascomata arising singly; ascospores with angular lumina; lichenized with *Trentepohlia* .... **Pyrenula** (p. 62)
– Ascomata arising in circular groups, opening through a common stromatic tissue; ascospores with rounded lumina; not lichenized .... **Dothivalsaria** (p. 56)

8 (4) Ascomatal opening a pore (ostiole); hymenium never exposed 9
– Ascomatal opening a broad circular disc, apothecium-like in surface view; hymenium exposed from an early stage; algicolous or lichenized .... **Lichenothelia** (p. 57)

9 (8) Ascomata immersed, only the ostiolar region exposed 10
– Ascomata erumpent and finally largely superficial 12

10 (9) Ascomata flask-shaped or globose, ascomatal wall always entire; lichenicolous 11
– Ascomata applanate, ascomatal wall almost always dimidiate; on bark, lichenized with *Trentepohlia* or not lichenized .... **Mycomicrothelia** (p. 64)

11(10) Ascomatal wall hyphal (textura intricata); ascomata united above by a clypeate tissue; not usually forming galls .... **Clypeococcum** (p. 53)
– Ascomatal wall cellular (textura angularis); ascomata not united above by a clypeate tissue; usually forming galls .... **Polycoccum** (p. 62)

12 (9) Pseudoparaphyses persistent; ascospore cells ± equal in length, usually verruculose, without strongly thickened walls 13
– Pseudoparaphyses deliquescing at maturity; ascospore cells usually unequal in length, smooth-walled, the walls conspicuously thickened .... **Splanchnonema** (p. 62)

13(12) Young ascomata ± globose; ascomatal wall usually evenly developed and extending below the ascomatal cavity, wall composed of rather large angular cells; centrum usually I−; mainly on wood .... **Kirschsteiniothelia** (p. 57)
– Young ascomata ± applanate; ascomatal wall less developed below, wall composed of small rounded cells; centrum I + blue; mainly on bark .... **Peridiothelia** (p. 120)

14 (3) Asci 4–8-spored, discharge fissitunicate, exclusively lichenicolous .... **Endococcus** (p. 56)
– Asci multispored, discharge by apical bursting; mainly lichenicolous .... **Muellerella** (p. 60)

Generic names

This section provides a synopsis of generic, subgeneric, and sectional names either used for *Microthelia*-like fungi or investigated in the course of this study. It must be stressed that this list does not purport to include all described genera of pyrenocarpous fungi (and lichens) reported as having brown one-septate ascospores produced in thick-walled or bitunicate asci.

Actinothecium Flotow in *Bot. Ztg* **13**: 130 (1855).

Introduced as a replacement name for *Tichothecium* Flotow and consequently automatically typified by the nomenclatural type of that genus (see p. 62) under Art. 7.9; the name is consequently a synonym of *Verrucaria* Schrader nom. cons.

Amphisphaeria Ces. & de Not. in *Comm. Soc. crittog. Ital.* **1**: 223 (1863), nom. cons.

Although sometimes used for many pyrenomycetes with one-septate brown ascospores, the genus is only correctly employed the Sphaeriales because the asci are unitunicate in structure and have an apical ring turning blue in iodine. The genus is in need of a monographic study, but descriptions and illustrations of several species are provided by Müller & von Arx (1962: 691–695).

The typification of *Amphisphaeria* is discussed by Hawksworth & Sherwood (1981), who proposed the adoption of *A. umbrina* (Fr.) de Not. as lectotype.

Anzia Garov. in *Rc. Ist. lomb. Sci. Lett.*, II, **1**: 558 (1868), nom. illegit. (Art. 64.1), non *Anzia* Stizenb. in *Flora, Jena* **44**: 393 (1861), nom. cons.

Type species: *A. aterrima* (Krempelh. ex Anzi) Garov.

Lichenothelia D. Hawksw. (see below) was introduced to replace this illegitimate generic name by Hawksworth (1981*b*).

Arnaudiella Petrak in *Annls mycol.* **25**: 339 (1927).

Type species: *A. genistae* (Fuckel) E. Müller

This generic name is mentioned here as it was applied to the species now called *Mycomicrothelia macularis* by Müller (1959). However, the type species of *Arnaudiella* is referrable to the Microthyriaceae Sacc. (see von Arx & Müller, 1975). Members of this family have entirely superficial scale-like ascomata with the upper parts composed of neatly radially orientated elongate ± rectangular cells; no pseudoparaphyses or other hamathecial filaments occur.

Astrosphaeriella Sydow & H. Sydow in *Annls mycol.* **11**: 260 (1913).

Type species: *A. fusispora* Sydow & H. Sydow (i.e. *A. stellata* (Pat.) Sacc.)

Figs 2A, 4A–C.

This generic name was used by Scheinpflug (1958) for a heterogeneous assemblage of four species and later treated as a synonym of *Microthelia* by Müller & von Arx (1962). The genus was re-investigated by Hawksworth (1981*a*) who found it to be melanommataceous; ten species are now known (Hawksworth & Boise, 1985) all of which are tropical and occur on palms and stems of bamboos and other stout grasses. The distinguishing features of the genus are summarized above (p. 48) and in Table 1. Names included in *Astrosphaeriella* or its synonymous genera (i.e. *Astrosphaeria* (Höhnel) Sydow, *Asterella* Hara [non (Sacc.) Sacc.], *Asterotheca* Hino, and *Astrotheca* Hino) and not also combined into *Microthelia* are omitted from the 'Excluded species' section of this paper as they are discussed by Hawksworth (loc. cit.).

Clypeococcum D. Hawksw. in *Bot. J. Linn. Soc.* **75**: 196 (1977).

Type species: *C. cladonema* (Weddell) D. Hawksw.

Fig. 5A–B.

This genus is similar to *Polycoccum* (see p. 62) from which it is separated by the hyphal ascomatal wall which spreads around the ostiole to form a clypeate structure often linking several ascomata. Four species are currently accepted in the genus, all of which are lichenicolous.

Cryptodidymosphaeria (Rehm) Höhnel in *Sber. Akad. Wiss. Wien, mat.-nat. Kl.* I, **126**: 359 (1917).

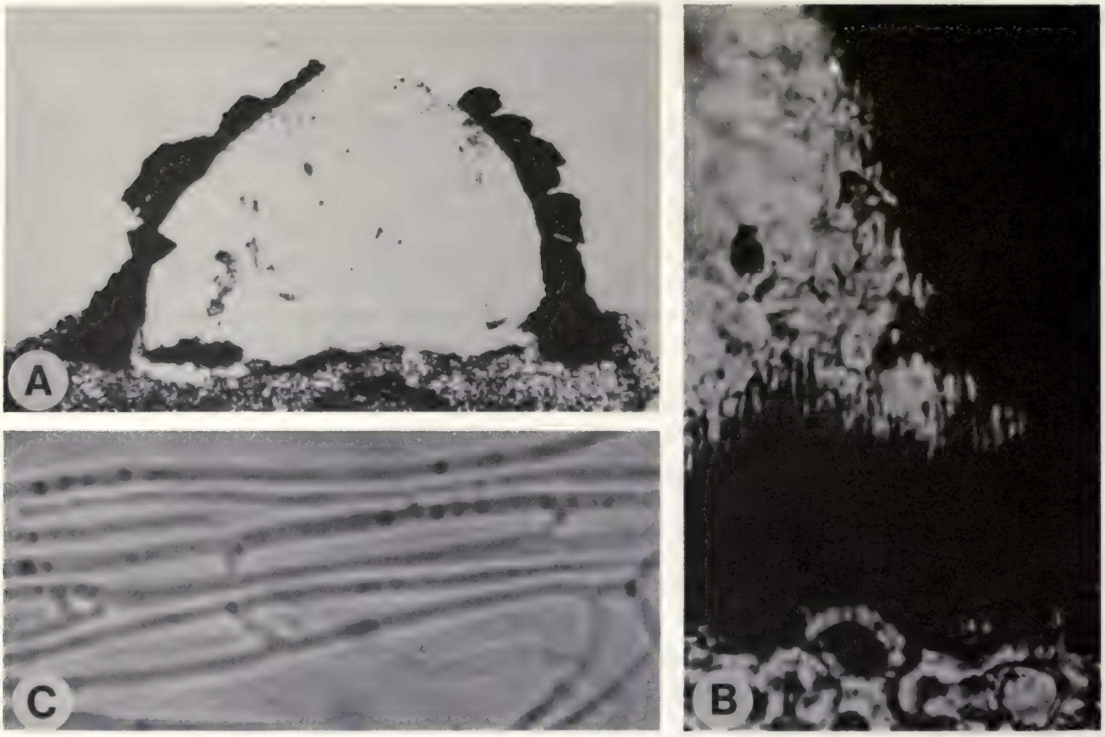

Fig. 4 *Astrosphaeriella*. **A**, Vertical section of ascoma of *A. stellata* (Pat.) Sacc. (S—holotype of *A. fusispora* Sydow & H. Sydow), × 100. **B**, Vertical section of ascoma of *A. trochus* (Penzig & Sacc.) D. Hawksw. showing the vertically orientated palisade of cells in the angles of the ascomatal cavity (PAD—holotype), × 1020. **C**, Paraphysoids (trabeculate pseudoparaphyses) in *A. stellata* (material as **A**), × 2500.

Type species: *C. conoidea* (Niessl) Höhnel

The genus is generally subsumed under *Didymosphaeria*, but its type probably occupies a rather isolated position. It has rather large superficial entire flask-shaped ascomata and occurs on decorticated wood; illustrations are provided by Scheinpflug (1958: 352, fig. 8).

Didymascina Höhnel in *Annls mycol.* **3**: 331 (1905).

Type species: *D. salicicola* (Allescher) Höhnel (i.e. *D. futilis* (Berk. & Broome) Rehm)

A synonym of *Didymosphaeria* s.str. as currently interpreted.

Didymosphaerella Cooke in *Grevillea* **19**: 3 (1890).

Type species: *D. filicina* Cooke

According to the original description of *Didymosphaerella filicina*, for which Saccardo (1891: 738) introduced the new name *Didymosphaeria pteridina* Sacc., this new Zealand species has globose papillate ascomata and cylindrical asci with uniseriately arranged ascospores; the ascospores are not constricted at the septum and said to be 8 × 5 μm. This genus was retained as a synonym of *Didymosphaeria* by Müller & von Arx (1962: 288) and, on the basis of this data, the fungus appears to be very close to if not synonymous with that genus.

Didymosphaeria Fuckel in *Jb. nassau Ver. Naturk.* **23/24**: 140 (1870).

Type species: *D. epidermidis* Fuckel (i.e. *D. futilis* (Berk. & Broome) Rehm)

Fig. 5C–D.

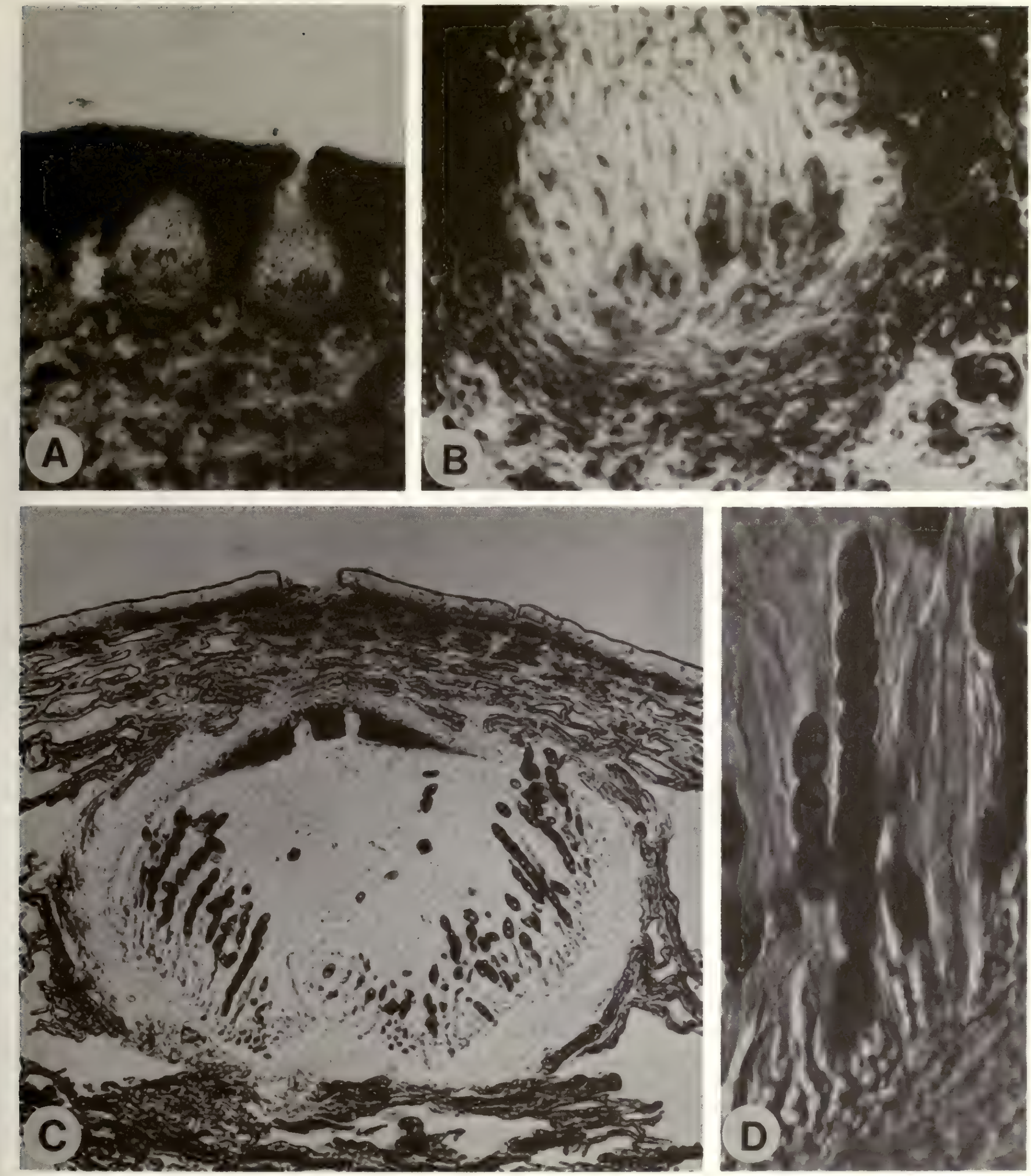

Fig. 5 **A**, Vertical section of ascomata of *Clypeococcum cladonema* (Weddell) D. Hawksw. on *Parmelia pulla* Ach. thallus (showing the clypeate structure joining the upper parts of the ascomata, IMI 212821), × 250. **B**, As **A** but showing detail of the hyphal ascomatal wall and pseudoparaphyses, × 1020. **C**, Vertical section of ascoma of *Didymosphaeria futilis* (Berk. & Broome) Rehm (IMI 33270) showing the hyaline walls pigmented only near the ostiolar region, × 250. **D**, As **C** but showing the detail of the hyphal ascomatal wall, paraphysoids, and cylindrical asci with uniseriately arranged ascospores, × 1020.

The genus was originally introduced for six species, *D. peltigerae* Fuckel, *D. galiorum* (Desm.) Fuckel, *D. epidermidis* (Fuckel) Fuckel, *D. genistae* Fuckel, *D. rubri* (Fr.) Fuckel, and *D. xylostei* (Pers.) Fuckel. As lectotypified by the species now known as *D. futilis*, however, the genus belongs to the Didymosphaeriaceae Barr, a melanommataceous family, and is characterized by trabeculate pseudoparaphyses (paraphysoids), immersed ascomata with hyphal walls becoming deeply pigmented and clypeate around the ostiole, and symmetrically 1-septate ascospores. With this circumscription, the genus is probably almost entirely confined to herbaceous stems. An illustration of the type species is provided by Scheinpflug (1958: 343 fig. 3), and a section of the species is included here as Fig. 5C. Scheinpflug's (1958) broad concept embraced taxa that need to be referred to several families and can no longer be maintained.

Didymosphaeria [subgen.] **Microthelia** Sacc., *Syll. Fung.* **1**: 709 (1882), as 'Körb., Niessl'.

In endeavouring to recognise Körber's genus *Microthelia* as a subgenus of *Didymosphaeria* Fuckel, Saccardo (loc. cit.: 715–716) specifically excluded *M. micula* and *M. atomaria*, and included the generally accepted type species of *Didymosphaeria*, *D. futilis* (Berk. & Broome) Rehm (as *D. epidermidis* (Fr.) Fuckel) in the subgenus *Microthelia*. As a result Saccardo has to be considered as having introduced a superfluous subgeneric name which must be rejected (Art. 63.1), automatically typified by the species now known as *D. futilis* (Art. 7.11), and attributed to Saccardo alone.

Dipyrenis Clem., *Gen. Fungi*: 173 (1909).

Pyrenula sect. *Pseudacrocordia* Müll. Arg. in *Flora, Jena* **68**: 333 (1885).

Type species: *D. brachysperma* (Müll. Arg.) Clem.

This genus was introduced by Clements (loc. cit.) for 'Pyrenula phaeodidyma', i.e. *Pyrenula*-like species with 1-septate ascospores. The holotype material was examined by Hawksworth (1985*c*) who found it to be in a poor state of preservation and not certainly even an ascomycete. The sporocarp structure, illustrated by Hawksworth (loc. cit.), is quite distinct from any of the other genera accepted in this revision.

Dothivalsaria Petrak in *Sydowia* **19**: 283 (1966 ['1965']).

Type species: *D. megalospora* (Auersw.) Petrak

This monotypic genus is referred to the Massariaceae by Barr (1979*b*) who provided a description and illustrations of the type species. The ascospores are rather thick-walled, the hamathecium consists of trabeculate pseudoparaphyses (paraphysoids), the ascomata arise in circular groups beneath a black stomatic tissue and have walls consisting of radially compressed rectangular rather pale brown cells. The genus is remote from others considered here.

Endococcus Nyl. in *Mém. Soc. imp. Sci. nat. Cherbourg* **3**: 193 (1855).

Type species: *E. rugulosus* Nyl.

This genus includes 13 lichenicolous species which have entire flask-shaped or subglobose ascomata, bitunicate asci which discharge fissitunicately, no interascal filaments, and 1-septate, brown, smooth-walled ascospores. See Hawksworth (1979*a*).

Haplovalsaria Höhnel in *Sber. Akad. wiss. Wien, mat.-nat. Kl.* I, **128**: 582 (1919).

Type species: *H. simplex* Höhnel

According to the original description, *H. simplex* has immersed and round ascomata which have periphyses and are united together into a whitish discoid stroma. I have not studied any material of this taxon, which was described from Java.

Jahnula Kirschst. in *Annls mycol.* **34**: 196 (1936).

Type species: *J. aquatica* (Plöttner & Kirschst.) Kirschst.

Fig. 2B.

This monotypic genus was placed as a synonym of *Microthelia* by Müller & von Arx (1962: 282) but differs from other accepted genera in the entire flask-shaped ascomata, the outer layers of which consist of massive (20–30 μm diam) pseudoparenchymatous cells. The fungus occurs on submerged wood in Germany and Switzerland (J. Webster, in litt.). A description and illustrations are included in Hawksworth (1984).

Kirschsteiniella Petrak in *Annals mycol.* **23**: 331 (1923).

Type species: *K. applanata* (Fr.) Petrak

In describing this genus, Petrak stated 'Typusart: *Kirschsteiniella applanata* (Fr.) Petr.' and cited *Sphaeria applanata* Fr. as a synonym. There can be little doubt from Petrak's description that the fungus he had in mind was that now referred to as *Kirschsteiniothelia aethiops* (see below). However the type material of Fries' name is a coelomycete belonging to the genus *Cyclothyrium* Petrak (see p. 134). Under Art. 10.2 as revised at the Sydney Congress (Voss et al., 1983) *Kirschsteiniella* must be regarded as a synonym of *Cyclothyrium*.

Kirschsteiniothelia D. Hawksw. in *Bot. J. Linn. Soc.* **91**: 182 (1985).

Type species: *K. aethiops* (Berk. & Curtis) D. Hawksw.

Figs 2C, 6A.

This new generic name was introduced by Hawksworth (loc. cit.) for *Kirschsteiniella* auct. non Petrak (see above). The distinguishing features of *Kirschsteiniothelia* are summarized in Table 1 and discussed above (p. 50). The genus includes six species, all of which appear to be saprophytic.

Lichenothelia D. Hawksw. in *Lichenologist* **13**: 142 (1981).

Type species: *L. scopularia* (Nyl.) D. Hawksw.

Figs 2D, 6B–D.

Introduced by Hawksworth (loc. cit.) as a new name to replace the illegitimate *Anzia* Garov. (see above). The distinguishing characters of the genus are summarized in Table 1 and its affinities are discussed in the preceding section (p. 48). It includes two species which are either algicolous or lichenized.

Massariellopsis Curzi in *Atti Ist. Bot. Pavia* **2** (3): 162 (1927).

Type species: *Massariellopsis aprutina* Curzi

The type species is generally regarded as conspecific with *Didymosphaeria oblitescens* (Berk. & Broome) Fuckel, which appears to be congeneric with the type species of *Didymosphaeria* s.str.

Massariopsis Niessl in *Verh. naturf. Ver. Brünn* **14**: 199 (1876).

Type species: Not designated

This genus is included because Niessl (1881) equated it with *Microthelia*, and Rehm (1906: 270) employed it for the species called *Mycomicrothelia wallrothii*. Seven species were mentioned in the original account of *Massariopsis*, but none appear to belong to any of the genera accepted in the present revision. *Amphisphaeria umbrina* (Fr.) de Not. was one included and the treatment of Müller & von Arx (1962: 691), who placed *Massariopsis* as a synonym of *Amphisphaeria* Ces. & de Not., is consequently satisfactory if there is no earlier lectotypification (see p. 53).

Microthelia Körber, *Syst. Lich. Germ.*: 372 (1855).

Pyrenula sect. *Microthelia* (Körber) Branth & Rostrup in *Bot. Tidsskr.* **3**: 259 (1869).
Non *Didymosphaeria* [subgen.] *Microthelia* Sacc. (1882) (see p. 56).
Verrucaria sect. *Microthelia* (Körber) Claudel & Harm., *Guide Elem. Lich.*: 77 (1904) [non vidi].
Microthelia [sect.] *Miculae* Jatta, *Fl. Ital. Crypt.* **3**: 897 (1911), nom. illegit. (Art. 63.1).
Microthelia sect. *Hemithelia* Vainio in *Ann. Acad. Sci. fenn.* A, **15** (6): 347 (1921), nom. illegit. (Art. 63.1).
Non *Microthelia* Vainio (1921) (see p. 59).

Type species: *M. micula* Körber (i.e. *Anisomeridium biforme* (Borrer) R. C. Harris)

Körber (loc. cit.) originally introduced this generic name for four species; the identities of which are reviewed above (p. 44). The first mentioned species, *M. micula*, has been consistently misapplied (see p. 157) but unanimously accepted as the lectotype species of the genus. According to Art. 10.2, the generic name *Microthelia* would become an earlier synonym for

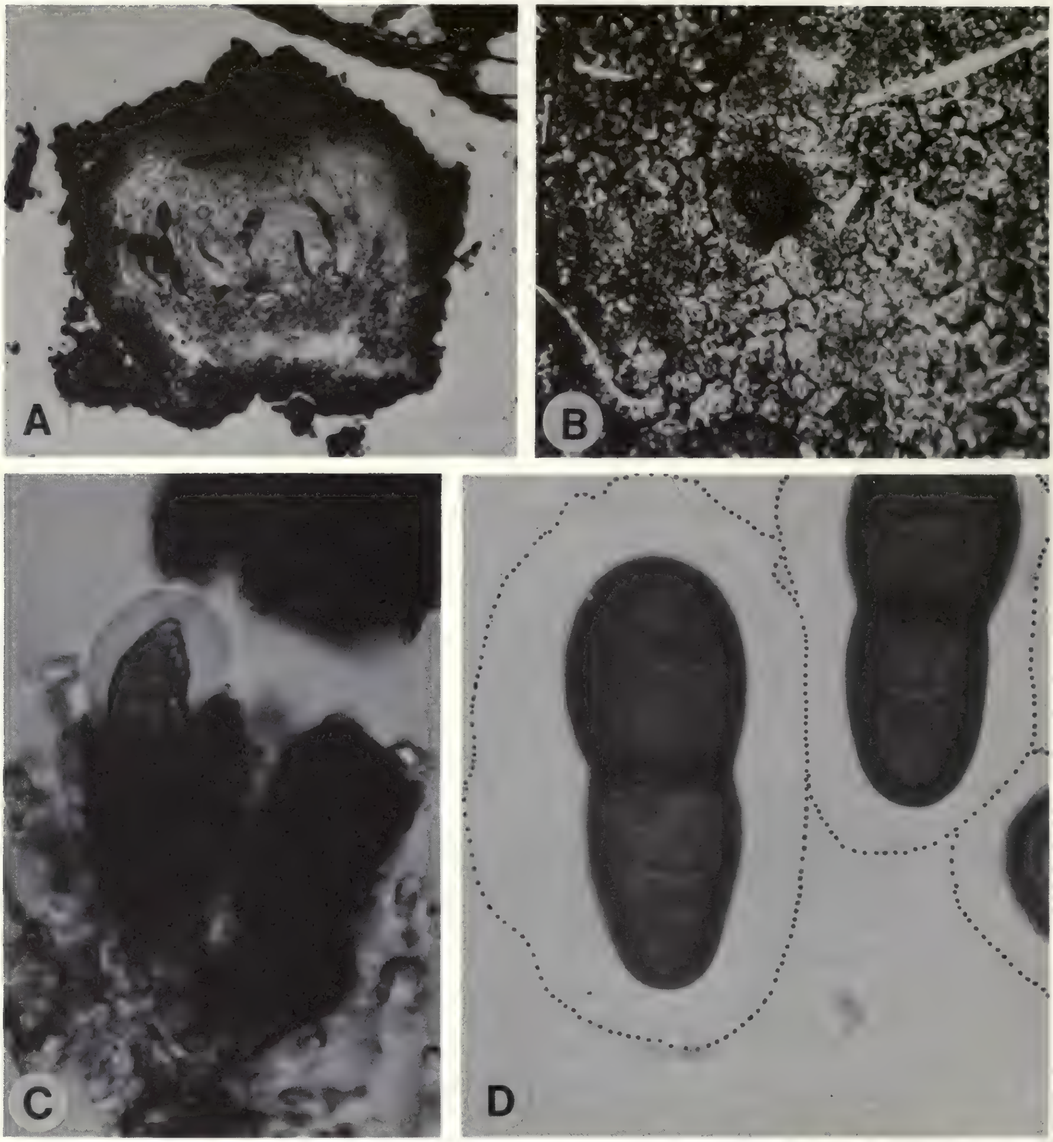

Fig. 6 **A**, Vertical section of ascoma of *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw. (DAOM 44956) showing the cellular ascomatal wall, pseudoparaphyses, and well-developed base, × 160. **B**, Surface view of ascoma and 'thallus' of *Lichenothelia metzleri* (Lahm) D. Hawksw. (L 910.195-373—holotype) showing the exposed disc-like hymenium, × 50. **C**, Discharging ascus of *L. metzleri* stained in Lugol's iodine to show the strong amyloid reaction of the outer ascus wall layers (CAN(L) 35819), × 1020. **D**, Ascospores of *L. metzleri* showing the thick-walls, development of secondary distosepta, and thick gelatinous sheaths (dotted) mounted in potassium hydoxide (material as **B**), × 2500.

Anisomeridium (Müll. Arg.) M. Choisy; the latter name has therefore been proposed for conservation against *Microthelia* (Hawksworth & Sherwood, 1981).

However, an important statement under the account of *M. pygmaea* has generally been overlooked in discussions of the nomenclature of this name. Körber (op. cit.: 374) states:

> 'Herr Massalongo hat auf Grund der vielsporigen Schläuche und der dyblastischen braunen Sporen in einem paraphysenlosen Nucleus für diese Flechte die Flotow'sche Gattung *Tichothecium* wieder

> aufgenommen, allein ich habe diese Bezeichnung nicht adoptirt, um eine Verwechselung mit der ähnlich klingenden Pilzgattung *Trichothecium* zu verhüten. Auch habe ich die Grenzen der von mir substituirten Gattung *Microthelia* beträchtlich erweiten und (um nicht zwei neue Gattungen ohne besondere Noth aufstellen zu müssen) in ihrer Diagnose von dem Merkmale der einerseits nur 8-sporigen, andrerseits vielsporigen Schläuche abstrahiren müssen.'*

This statement strongly indicates that Körber intended *Microthelia* as a replacement for *Tichothecium* Flotow, non *Trichothecium* Link. If this is accepted *Microthelia* automatically becomes an additional synonym of *Verrucaria* Schrader nom. cons. (see p. 62). A complicating factor in this interpretation is that Körber (1855: 342) indicated that *V. nigrescens* was the type species of *Tichothecium* and treated that as a synonym of *V. fuscoatra*, within *Verrucaria*. This being so, it might be argued that Körber was introducing a generic name for *Tichothecium* sensu Massalongo, not sensu Flotow, but I think this must be discounted as Körber speaks of 'Flotow'sche Gattung *Tichothecium*'.

The inclusion of the sectional names *Miculae* and *Hemithelia* in the synonymy given above presumes *M. micula* to be accepted as the type of *Microthelia*.

Microthelia Vainio in *Acta Soc. Fauna Fl. fenn.* **49** (2): 144 (1921), nom. illegit. (Art. 64.1), non *Microthelia* Körber, *Syst. Lich. Germ.*: 372 (1855) (q.v.).

Type species: *M. scopularia* (Nyl.) Blomb. & Forss.

Vainio (loc. cit.) excluded the type species of Körber's genus (i.e. *M. micula*) which he referred in *Didymosphaeria*. Vainio must consequently be interpreted as introducing a new generic name typified by one of the species he included. The genus consequently becomes a synonym of *Lichenothelia* D. Hawksw. (Hawksworth, 1981*b*).

Microthelia [sect.] **Atomariae** Jatta, *Fl. Ital. Crypt.* **3**: 897 (1911).

Type species: *M. atomaria* (Ach.) Körber

The species on which this section was based strictly belongs to *Leptorhaphis* (see p. 135). The sectional name is therefore a synonym of *Leptorhaphis*.

Microthelia [sect.] **Ecatonosporae** Jatta, *Fl. Ital. Crypt.* **3**: 897 (1911).

Type species: *M. ecatonospora* Anzi

This sectional name is a synonym of *Muellerella* Hepp ex Müll. Arg. since *M. ecatonospora* proves to belong to that genus (see p. 146).

Microthelia sect. **Holothelia** Vainio in *Annls Acad. Sci. fenn.* A, **15** (6): 347 (1921).

Type species: *M. palavana* Vainio

Vainio probably intended this sectional name to include all species of *Microthelia* previously recognized with entire ascomata (see p. 46), but only *M. palavana* was mentioned in the original description and that must therefore be regarded as the holotype of this sectional name. The sect. *Holothelia* must consequently be treated as a synonym of *Acrocordia* Massal. since *M. palavana* belongs to that genus (see p. 159).

Microthelia [sect.] **Membranaceae** Jatta, *Fl. Ital. Crypt.* **3**: 897 (1911).

Type species: *M. membranacea* Anzi

This name was introduced for two species: *M. versispora* Bagl. & Car., here referred to *Polycoccum* (see p. 173), and *M. membranacea* Anzi, which is of uncertain application (see p. 156); the correct application of the sectional name is consequently also uncertain.

Microtheliomyces Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittogam. Pavia* V, **10**: 59 (1953).

Type species: *Microthelia atomaria* (Ach.) Körber

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* *Translation:* 'Based on the multispored asci and the dyblastic brown spores in a paraphyses-less nucleus, Mr Massalongo re-admitted this lichen into the genus *Tichothecium* of Flotow. I did not adopt this term, so as to avoid a confusion with a similarly sounding fungal genus *Trichothecium*. I also expanded the range of the genus *Microthelia* (substituted by me) considerably and (so as not to establish two new genera), I separated the characteristics of the 8-spored asci on the one hand and the multispored on the other.'

This generic name was introduced for the fungal element of *Microthelia* auct., but these authors typified their genus by '*M. atomaria* Krb.' (loc. cit.: 32). As the name *M. atomaria* was misapplied, and is strictly a *Leptorhaphis* species (see p. 135), Art. 10.2 requires that *Microtheliomyces* be added to the synonymy of *Leptorhaphis*.

Microtheliopsis Müll. Arg. in *Flora, Jena* **73**: 195 (1890).

Microthelia subgen. *Microtheliopsis* (Müll. Arg.) Vainio in *Acta Soc. Fauna Fl. fenn.* **7** (2): 232 (1890).
Microtheliopsidomyces Cif. & Tom. in *Atti Ist. bot. lab. Crittog. Pavia* V, **10**: 34 (1953), nom. illegit (Art. 63.1).

Type species: *M. uleana* Müll. Arg.

This genus was reported to differ from *Microthelia* in the alga present. A critical re-examination of the foliicolous *M. uleana* by Santesson (1952: 133–136) showed that in this algicolous or primitively lichenized fungus the cone-like ascomata had a separate spreading outer layer as well as an inner applanate sphere, both formed of interwoven dark-brown hyphae. Contrary to the original description of the genus, Santesson could find no paraphyses. The asci are thin-walled and the ascospores 3-septate, fusiform, and pale brown.

Microtheliopsis is unrelated to the other taxa treated in this paper, and Schilling (1927: 290) was not justified in placing *M. uleana* in *Microthelia*. Santesson (1952: 135) tentatively referred the genus to the Pyrenulaceae s. lat., but a more accurate appraisal of its affinities must await more detailed information on the structure of the ascus.

Muellerella Hepp, *in* Müller Argoviensis in *Mém. Soc. phys. Hist. nat. Genève* **16**: 419 (1862).

Type species: *M. polyspora* Hepp

This genus has subglobose ascomata with entire walls which lack interascal filaments and forms multi-spored asci with ascospores which are pale to dark-brown, smooth-walled, and 0–3 septate (see Hawksworth, 1979*a*). The genus includes about 10 species, all of which are probably lichenicolous.

Mycomicrothelia Keissler, *Rabenh. Krypt-Fl.* **9**, 1 (2): 23 (1936).

Type species: *M. macularis* (Hampe ex Massal.) Keissler

Figs 2F–G, 8–46.

The distinguishing characters of this genus, treated in detail below (pp. 64–120), are summarized in Table 1 and discussed further on p. 48.

Pemphidium Mont. in *Ann. Sci. nat.* (Bot.) II, **14**: 329 (1840).

Type species: *P. nitidum* Mont.

The type species was found by Leprieux on the petioles of the palm *Maximiliana regia* in 1837. Von Arx & Müller (1954: 396) stated that *Astrosphaeriella* was a later synonym of *Pemphidium*, but this was disputed by Scheinpflug (1958: 369) who considered *P. nitidum* to belong to the Sphaeriales. Examination of an isotype of *P. nitidum* in K (*Leprieux* 391) confirmed Scheinpflug's interpretation. The asci are not bitunicate but thin-walled, with a very small apical thickening giving the lumen an apex which appears squared; no apical apparatus could be demonstrated. The ascospores of *P. nitidum* recall those of *A. stellata* (Pat.) Sacc. in shape but are less constricted centrally, hyaline and often simple (sometimes 1-septate) at maturity. The ascomata are subepidermal, applanate, and with a spreading involucrellum as correctly figured by both Montagne (loc. cit.: Pl. 19 fig. 10m–q) and von Arx & Müller (1954: 396 fig. 118); their superficial appearance consequently differs markedly from that characteristic of *Astrosphaeriella* (see Figs 2A, 4A).

Peridiothelia D. Hawksw. in *Bull. Br. Mus. nat. Hist.* (Bot.) **14**: 120 (1985).

Type species: *P. fuliguncta* (Norman) D. Hawksw.

Figs 2E, 47–52.

The distinguishing characters of this genus, treated in detail below (pp. 120–130), are summarized in Table 1 and discussed further on p. 50.

Phaeothyriolum H. Sydow in *Annls mycol.* **36**: 305 (1938).

Type species: *P. eucalyptinum* H. Sydow

This generic name was placed as a synonym of *Mycomicrothelia* by Müller & von Arx (1962: 324) but, as I have not been able to examine any material of the type species (see p. 146), it is not treated further here.

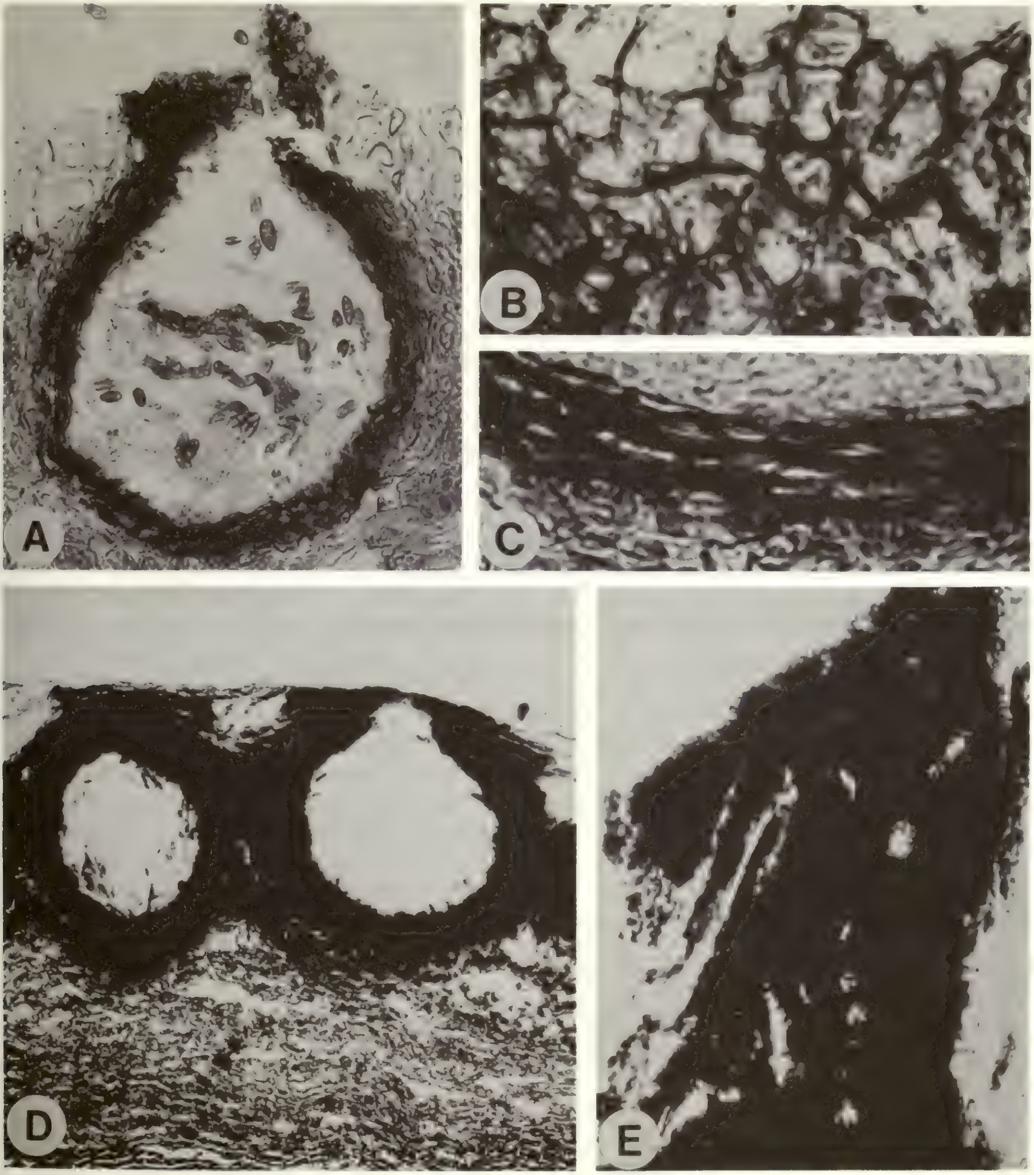

Fig. 7 **A–C**, *Polycoccum peltigerae* (Fuckel) Vězda on *Peltigera rufescens* (Weis) Humb. thallus (IMI 189658); **A**, vertical section of ascoma showing the uniformly thickened wall, × 250; **B**, surface view of ascoma wall showing the polyhedral pseudoparenchymatous cells, × 1020; **C**, vertical section of ascoma wall showing cells as in B in side view, × 1020. **D–E**, *Pyrenula chlorospila* (Nyl.) Arnold (IMI s.n.); **D**, vertical section of ascomata showing the uniformly thickened walls, × 100; **E**, vertical section of upper part of ascoma wall showing the clypeate structure incorporating periderm cells, × 500.

Polycoccum Sauter ex Körber, *Parerg. Lich.*: 470 (1865).

Type species: *P. sauteri* Körber (i.e. *P. trypethelioides* (Th. Fr.) R. Sant.)

Fig. 7A–C.

The ascomata in *Polycoccum* are characteristically subglobose or flask-shaped, entire and composed of angular pseudoparenchymatous cells (textura angularis), and the ascomatal cavity includes branched and anastomosing cellular pseudoparaphyses. The ascospores are 1-septate, often unequal-celled, dark brown and either smooth or verruculose. About 20 species are known, all of which are lichenicolous, many forming conspicuous galls on the host lichens.

Polythelis Clem., *Gen. Fungi*: 173 (1909).

Type species: *P. sexlocularis* (Müll. Arg.) Clem.

The type species of this genus, introduced for *Microthelia*-like species with multiseptate ascospores, belongs to the Pyrenulaceae. *P. sexlocularis* was discussed and illustrated by Hawksworth (1983*b*) and is treated further below (p. 165).

Pyrenula Massal., *Rich. Auton. Lich. Crost.*: 162 (1852).

Type species: *P. nitida* (Weigel) Ach.

Fig. 7D–E.

The genus name has been proposed for conservation as above by Hawksworth & Sherwood (1981: 346). The genus has ascomata with trabeculate pseudoparaphyses (paraphysoids) at first and later true paraphyses, and distoseptate ascospores with angular lumina. Most species have multiseptate ascospores, but the genus has caused some confusion with *Microthelia*-like taxa as there are some tropical species with 1-septate ascospores.

Rhynchostomopsis Petrak & H. Sydow in *Annls mycol.* **21**: 377 (1923).

Type species: *Rhynchostomopsis brasiliensis* (Höhnel) Petrak & H. Sydow

According to the original description, the ascomata in this fungus are composed of isodiametric cells and the asci are elongate-cylindrical with ± uniseriately arranged ascospores 7–11 × 3–4 μm. It is probably close to if not synonymous with *Didymosphaeria*.

Splanchnonema Corda *in* Sturm, *Deutschl. Fl.* **2** (9), 3: 715 (1829).

Type species: *Splanchnonema pustulatum* Corda

Species of this genus have thick-walled distoseptate asymmetrical ascospores with one or more septa. The ascomata are usually immersed and entire with a hamathecium of cellular pseudoparaphyses which are finally deliquescent. *S. melanterum* (J. B. Ellis & Everh.) Barr (see p. 156) shows some similarity in the form of the ascomata to *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw., but the very thick-walled smooth ascospores and structure of the peridium set it apart. The genus is referred to the Pleomassariaceae by Barr (1982), who provides an account of the 12 known North American species.

Tichothecium Flotow in *Bot. Ztg* **8**: 361 (1850).

Type species: *Verrucaria nigrescens* Pers.

The typification and nomenclature of this generic name were considered by Hawksworth (1979*a*) who showed that it must be treated as a superfluous name for *Verrucaria* Schrader, nom. cons.

Species concepts

Taxonomy

The main characters found to be of value for the separation of species within *Mycomicrothelia* are those derived from the structure of the ascomata and the ascospores; within *Peridiothelia* the ascomatal structure is rather constant and ascospores assume paramount importance. In both genera ascomatal dimensions and superficial appearance are also of value.

The ascomata in *Mycomicrothelia* consist of two tissues, an exciple which encloses the generative locule and an involucrellum composed of hyphae interspersed with host cells. The relative development of these two tissues differs significantly between species, as already noted above (p. 48), but the shape and extent of involvement of host cells in the involucrellum may be influenced by the nature of the bark itself. The extension of the involucrellum hyphae beyond the limits of the generative locule results in a distinct basal fringe which is a useful additional character for the separation of species. In general the exciple is less well-developed when there is a substantial involucrellum, and this is especially so below the centrum tissues when it is often absent or reduced to a few irregular brownish hyphae. The involucrellum in *Mycomicrothelia* characteristically turns shades of olivaceous green or olivaceous brown, depending on the species, when mounted in 10% potassium hydroxide; in *Peridiothelia* species no such colour change occurs.

The asci vary in size between species, and also to some extent in the degree to which they are clavate. In general they arise directly from the base of the generative locule but in some species they predominantly arise from the angles of the locule. The hamathecium consists of true pseudoparaphyses (Eriksson, 1981: 15) in both genera but, apart from some small variations in thickness, these appear to be of little diagnostic value below the rank of genus in *Mycomicrothelia* and *Peridiothelia*. More important are colour changes with iodine (after pre-treatment with 10% potassium hydroxide); in *Peridiothelia* species the centrum consistently turns deep blue, while in *Mycomicrothelia* no blue reaction has been found to occur. However, *M. atlantica* gives a patchy violet reaction which is similar to that noted in host cells infected with hyphae around the involucrellum of *M. willeyana*, in the fringe in *M. modesta*, and also, according to Harris (1973: 27), at the base of the ascomata in *M. wallrothii*.

The size and shape of the ascospores, the relative sizes of cells, rounding of the apices, degree of constriction at the septum, and the degree of development of verruculose ornamentation, provide the most valuable characters for species separation. The extent of the development of any gelatinous sheath is rather difficult to assess in old herbarium material and is certainly of supportive value in some species separations in *Mycomicrothelia*, but is hardly developed in any of *Peridiothelia*.

No anamorph has been found associated with *Peridiothelia* species, but several of *Mycomicrothelia* are regularly found with pycnidia intimately mixed amongst the ascomata. The pycnidia usually recall the ascomata in structure and reaction with potassium hydroxide. The conidia are generally bacillariform and simple but in *M. melanospora* they are brown and 1-septate, and in *M. wallrothii* simple, brown and with centrally thickened walls; the bacillariform hyaline conidia and the larger brown conidia may have different biological roles.

Secondary metabolites are not known to be of taxonomic importance within the Arthopyreniaceae and Phaeosphaeriaceae and were not investigated in this survey.

Characters can also be obtained from the thallus as a whole. A distinctive almost superficial creamy-white thallus is seen in some tropical species (e.g. *M. thelena*), in some a whitish patch on the bark is produced due to air being trapped below the surface layers of the periderm (e.g. *M. confusa*), but in the majority the superficial appearance of the host is unchanged (e.g. *M. macularis*). Distinctive black or purplish-black marginal zone lines delimit the extent of colonies in some *Mycomicrothelia* species.

The European species accepted here are generally well-separated by a combination of different characters, but in deciding on the circumscription of many tropical species a shortage of material was a severe constraint. In particular, the extent of variation in ascomatal size or ascospore size and shape within species was difficult to assess. As to adopt broad concepts could obscure differences which might be substantiated by later collections, it is more appropriate here to retain some rather similar taxa as separate species on the basis of small differences in ascospore shape or size with the recognition that some may eventually prove to require reduction to synonymy. I hope that this revision will stimulate further collection and study of this group of fungi and so assist in the clarification of the species concepts adopted here.

Biological concepts

The genus *Mycomicrothelia*, in common with *Arthopyrenia*, appears to include species which vary in their nutritional requirements. Species with a relatively well-developed thallus, such as *M. thelena*, appear to be regularly lichenized, while in many the nature of the relationship with a photobiont is less certain but probably regular (e.g. *M. confusa*), and some appear never to be lichenized (e.g. *M. melanospora, M. macularis, M. wallrothii*). Species in the latter category are generally extremely restricted with regard to their hosts, those in the intermediate category less so, and certainly lichenized species are probably not so host limited.

In all cases there is an intimate association between the host cells and the hyphae, which regularly penetrate the cells; so it may be that some nutrients are derived from the host in almost all species.

Detailed biological studies require fresh material as *Trentepohlia* or other algae involved are difficult to detect when dead as they lose their normal pigments.

As *Mycomicrothelia* appears to be a good example of a genus crossing biological boundaries (Hawksworth, 1978*a*; Hawksworth & Hill, 1984) it would be of interest to study and compare the nutritional requirements in different groups of species within the genus.

I. MYCOMICROTHELIA Keissler

Rabenh. Krypt.-Fl. **9**, 1 (2): 23 (1936).

Ascomata arising singly or rarely confluent, immersed, subperidermal or subepidermal, dark brown to black, dimidiate, usually applanate, ostiolate, ostiole usually depressed; involucrellum composed of irregularly radiating reddish-brown hyphae, hyphae olivaceous green or olivaceous brown in potassium hydroxide, hyphae intermixed with the host cells often binding them into a robust clypeate tissue, the host cells often penetrated and becoming occluded, the involucrellum extending beyond the ascoma to produce a distinct basal fringe in some species; exciple composed of reddish brown hyphae radially compacted to form a textura intricata, sometimes almost pseudoparenchymatous in parts, not or poorly developed below the generative locule; centrum not turning blue in iodine, but the centrum or other tissues giving a violet colour with iodine in a few species. *Hamathecium* consisting of pseudoparaphyses; pseudoparaphyses persistent, cellular, filamentous, branched and anastomosing. *Asci* arising from the base and(or) angles of the ascomatal cavity, elongate-clavate or broadly clavate to almost subcylindrical, short-stalked, bitunicate, with an internal apical beak, discharge fissitunicate, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid or soleiform, 1- or rarely 3-septate, constricted at the septum or not, upper cell usually larger, mainly olivaceous brown, apices rounded or somewhat attenuated, usually verruculose, with a thin gelatinous sheath often swelling markedly in potassium hydroxide.

Anamorph, when present, a pycnidial conidioma. *Conidiomata* globose, often recalling the ascomata in structure. *Conidiogenous cells* elongate-ampulliform, unbranched, phialidic. *Conidia* **either** bacillariform simple and hyaline, **or** ellipsoid, 1-septate and brown, **or** ellipsoid, simple with centrally thickened walls and brown.

Type species: Mycomicrothelia macularis (Hampe ex Massal.) Keissler (lectotype designated here). Two species were specifically mentioned when the generic name *Mycomicrothelia* was introduced by Keissler (loc. cit.: 33, 37), *M. atomaria* (Ach.) Keissler and *M. macularis*. *M. atomaria* was selected by Müller & von Arx (1962: 324), but this choice is unacceptable as that name is currently applied to a species of *Leptorhaphis* (see p. 135) and is therefore not in accordance with Keissler's protologue. *M. macularis* is consequently designated here as the lectotype for this generic name.

Number of species: Twenty-six species are accepted in this treatment, but more may be expected to be found, especially in the tropics where the largest numbers of species occur.

Hosts: On the outer bark layers of deciduous, or more rarely coniferous, trees or shrubs. Individual species are often restricted to one or a few hosts. Lichenized (usually or always) with *Trentepohlia*, doubtfully lichenized, or not lichen-forming and then saprophytic.

Distribution: Probably cosmopolitan in humid tropical to temperate regions, avoiding arid regions. Species are known from all continents apart from Antarctica.

Observations: Mycomicrothelia is referrable to the family Arthopyreniaceae W. Watson. Its affinities and separation from superficially similar genera are discussed separately above (pp. 47–50).

Keissler (loc. cit.: 23) gave a very short diagnosis of his new genus, 'Est *Didymosphaeria* peritheciis dimidatis', and used the name as an alternative to *Microthelia* for those who wished to use different generic names for non-lichenized species otherwise congeneric with lichen-forming taxa. As originally proposed *Mycomicrothelia* was consequently an 'alternative name' in the sense of Art. 34.4 but as it appeared before 1 January 1953 it must be accepted as validly published (Voss *et al.*, 1983: 34).

Key to the species

1 Ascospores mainly exceeding 20 μm in length 2
– Ascospores mainly less than 20 μm in length 10

2 (1) Ascospores mainly exceeding 7 μm in width 3
– Ascospores 17–22(–24) × 5·5–7·5 μm; ascomata 200–350 μm diam; New Zealand .... **16. M. minutissima** (p. 101)

3 (2) Ascospores mainly exceeding 10 μm in width 4
– Ascospores mainly less than 10 μm in width 7

4 (3) Ascospore apices rounded 5
– Ascospore apices attenuated; ascospores (22–)24–28(–29.5) × (8·5–)9–11·5(–12·5) μm; ascomata (300–)350–450(–500) μm diam; Colombia .... **2. M. apposita** (p. 68)

5 (4) Ascomata remaining largely immersed, low hemispherical to mammiform 6
– Ascomata becoming largely superficial, steeply cone-shaped, (250–)300–400(–450) μm diam; ascospores 19–23(–27) × (7·5–)9–11(–12) μm; India (Andaman Islands) .... **7. M. conothelena** (p. 81)

6 (5) Ascospores (21–)22–28(–30) × (8·5–)9–11(–12) μm, occasionally 3-septate; ascomata (250–)300–400 μm diam; Australia (Queensland) .... **20. M. obovata** (p. 106)
– Ascospores (17.5–)21–24(–26) × (7·5–)9–11·5(–13) μm, consistently 1-septate; ascomata (250–)300–400(–450) μm diam; Central and South America .... **24. M. thelena** (p. 112)

7 (3) Ascomata arising singly, not united by a common basal fringe 8
– Ascomata arising in groups of 2–8, united by a common basal fringe to 400 μm wide, (250–)300–400(–500) μm diam; ascospores (21–)22–25 × 7·5–9(–10·5) μm; South Africa .... **5. M. confluens** (p. 75)

8 (7) Ascospores rarely exceeding 22 μm in length 9
– Ascospores (21–)24–28(–30) × 7·5–9(–11) μm; ascomata 200–350(–400) μm diam; Central and South America .... **11. M. hemisphaerica** (p. 86)

9 (8) Ascomatal fringe well-developed, lenticular, to 350 μm broad; ascomata 200–300 μm diam, involucrellum 60–100 μm thick; ascospores 18–22 × (7·5–)8·5–10·5 μm; Europe and North America .... **12. M. inaequalis** (p. 90)
– Ascomatal fringe poorly developed, to 25 μm broad; ascomata (200–)250–300 μm diam, involucrellum 20–35 μm thick; ascospores (17·5–)19–22(–23) × (8–)8·5–10(–10·5) μm .... **18. M. modesta** (p. 104)

10 (1) Ascospores mainly exceeding 16 μm in length 11
– Ascospores mainly less than 16 μm in length 21

11(10) Ascomata rarely exceeding 350 μm diam 12
– Ascomata (200–)300–500(–550) μm diam; ascospores 16–19·5 × 7·5–10(–10·5) μm, lower cell *c.* ⅓ the length of the upper; on *Mimulus*, North America ... **8. M. dothideaspora** (p. 82)

12(11) Ascomata usually exceeding 200 μm diam 13
– Ascomata (100–)150–200(–250) μm diam, basal fringe well-developed to 100 μm wide; ascospores 15–20 × 6–9 μm; Central America .... **22. M. socialis** (p. 110)

13(12) Basal fringe of the ascomata extending at least to 50 µm 14
– Basal fringe of the ascomata not or scarcely extended 18

14(13) Basal fringe not exceeding 125 µm wide 15
– Basal fringe to 300 µm wide; ascomata 150–250(–300) µm diam; ascospores (12–)14–18 (–20) × 6–8(–8·5) µm; conidia doliiform, walls thickened centrally to polarilocular, brownish, (9–)11–12·5(–14) × 4–6·5 µm; on *Betula* (rarely *Populus*), Europe and North America .... **25. M. wallrothii** (p. 115)

15(14) Ascospores mainly exceeding 17 µm in length 16
– Ascospores 14·5–17·5(–19) × 6–7·5 µm; ascomata (200–)250–350(–400) µm diam; Cuba .... **15. M. miculiformis** (p. 99)

16(15) Conidiomata (pycnidia) intermixed with the ascomata 17
– Conidiomata (pycnidia) absent; ascospores (15·5–)17–19(–23) × 5–7 µm, scarcely constricted at the septum; ascomata (150–)200–250(–300) µm diam; Venezuela .... **1. M. anonacea** (p. 67)

17(16) Ascospores 17–22(–24) × 5·5–7·5 µm; ascomata 200–350 µm diam; conidiomata 75–100 µm diam; conidia 4–5 × 1–1·5 µm; New Zealand .... **16. M. minutissima** (p. 101)
– Ascospores 17–20(–21) × 7–8(–9) µm; ascomata 200–300 µm diam; conidiomata 50–75 µm diam; conidia 3–4 × 1–1·5 µm; on *Fraxinus*, North America .... **26. M. willeyana** (p. 119)

18(13) Ascospore apices markedly attenuated, at least in the lower cell 19
– Ascospore apices broadly rounded, ascospores (15–)16–18 × (6·5–)7–8(–9) µm; Europe .... **21. M. pachnea** (p. 108)

19(18) Ascospores mainly less than 7·5 µm wide 20
– Ascospores (15·5–)17·5–21(–25) × (6–)7–9(–10) µm; ascomata 200–300(–400) µm diam; thallus whitish; mainly on *Corylus*, Western Europe .... **6. M. confusa** (p. 76)

20(19) Ascomata 120–150 µm tall; ascospores (14–)15·5–17·5 × (6–)6·5–7·5 µm; India (Kerala) .... **19. M. nonensis** (p. 105)
– Ascomata 150–225 µm tall; ascospores (13·5–)17–19(–21) × (5·5–)6·5–7·5(–8·5) µm; Central and South America .... **4. M. captiosa** (p. 73)

21(10) Ascospores mainly exceeding 5·5 µm in width 22
– Ascospores 12·5–14(–15·5) × 4–5·5 µm; ascomata (150–)200–250 µm diam; Cuba .... **9. M. exigua** (p. 84)

22(21) Conidiomata (pycnidia) intermixed with the ascomata 23
– Conidiomata (pycnidia) absent 25

23(22) Conidia bacillariform, hyaline 24
– Conidia ellipsoid, 1-septate, brown, 13–14·5 × 5·5–6·5 µm; ascospores (12·5–)13·5–15·5 (–17) × (6–)6·5–7·5(–8) µm; on *Mespilus*, Europe .... **14. M. melanospora** (p. 95)

24(23) Ascomata 100–175(–200) µm diam; ascospores (11·5–)12·5–15(–17·5) × (4–)5–6(–7) µm; conidia 5–8 × 0·7–1·5 µm; on *Daphne* and *Ribes*, central Europe ... **13. M. macularis** (p. 92)
– Ascomata (150–)200–300(–350) µm diam; ascospores (12·5–)13·5–16(–17·5) × (5·5–)6·5–8(–9) µm; conidia 3–4 × 0·5–0·7 µm; on *Corylus*, western Ireland and Scotland .... **3. M. atlantica** (p. 70)

25(22) Ascomata with a basal fringe to 50 µm broad 26
– Ascomata lacking a distinct basal fringe, (125–)160–200(–275) µm diam; ascospores (12·5–)13·5–15(–16) × (5·5–)6–6·5(–7) µm; China .... **17. M. minutula** (p. 102)

26(25) Ascospore apices somewhat attenuated; ascospores (11–)12–14(–15) × (5–)5·5–6·5(–7·5) µm; China and Japan .... **10. M. fumulosa** (p. 86)
– Ascospore apices rounded; ascospores 13·5–16 × 6–7 µm; Cuba ...... **23. M. subfallens** (p. 111)

The species

1. **Mycomicrothelia anonacea** (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia anonacea Müll. Arg. in *Hedwigia* **34**: 145 (1895).

Fig. 8A–C.

Ascomata arising singly, scattered, colonies scarcely delimited and bark not conspicuously discoloured, margins not seen, immersed, subepidermal, the epidermis raised to form low

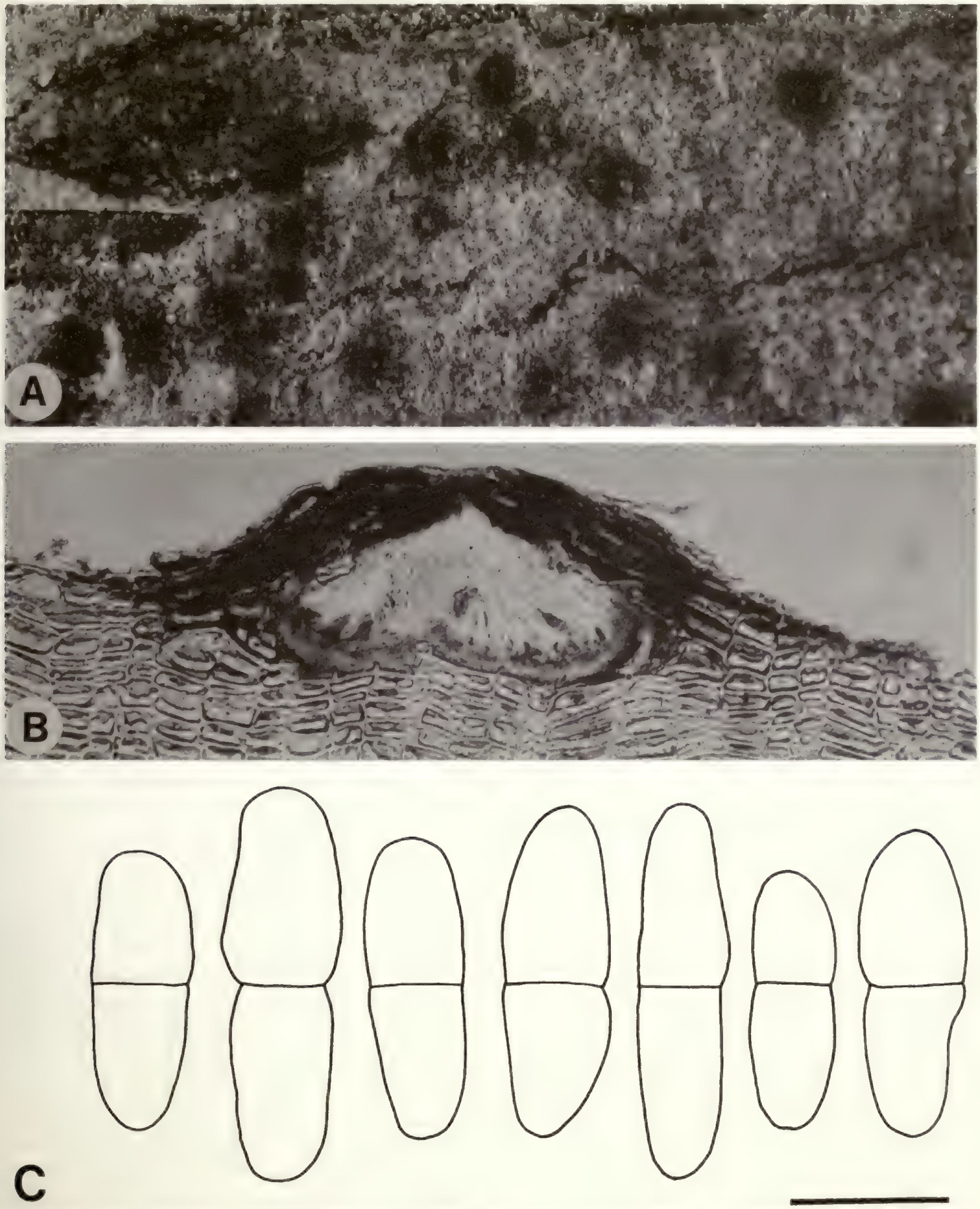

Fig. 8 *Mycomicrothelia anonacea* (G–lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

hemispherical projections, only the ostiole completely exposed, black; individual ascomata dimidiate, (150–)200–250(–300) μm diam, (80–)100–170 μm tall, basal fringe well-developed forming a circular ring mainly 50–100 μm wide, ring dark grey but becoming olivaceous in potassium hydroxide, ostiole depressed, minute, the centrum often visible as a white central spot, 20–30 μm diam; involucrellum dark reddish brown, becoming distinctly olivaceous in potassium hydroxide, 30–50 μm thick, consisting of host cells intermixed with fungal hyphae, hyphae irregularly radially orientated, 2–3(–3·5) μm thick, uneven, richly branched, smooth-walled, mainly between the cells of the host but sometimes penetrating them; exciple variable in development, in older ascomata mainly 5–15 μm thick, composed of a variable number of layers of densely interwoven hyphae similar in colour to those in the involucrellum and 2–3 μm wide (textura intricata), this layer continuous with the base of the locule but there thinner and uneven, reduced to only a single layer of hyphae about 3 μm thick in places which is also somewhat paler in colour; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, sparsely septate, branched and occasionally anastomosing, (1·5–)2–3 μm thick. *Asci* not seen in a mature condition, bitunicate. *Ascospores* distichously arranged in the asci, oblong-ellipsoid, 1-septate, slightly constricted at the septum, cells almost equal in size, the apices rather abruptly rounded and truncated, cells tending to have central indentations, olivaceous brown, verruculose, with a distinct gelatinous sheath to 2 μm thick in potassium hydroxide, (15·5–)17–19(–23) × 5–7 μm.

Anamorph: Unknown.

Host: Anona muricata bark. Apparently not lichenized.

Distribution: Venezuela. Known only from the type collection.

Observations: The oblong-ellipsoid spores and distinct basal fringe of the ascomata make this species particularly easy to recognize. It has an obvious affinity with *Mycomicrothelia wallrothii* in the structure of the ascomata but differs in the ascospore shape and width, circular fringe, absence of an anamorph, and disparate hosts.

Specimen: **Venezuela:** Caracas, 'in trunco *Anonae muricatae*', 1878, *Ernst* (G—holotype).

2. **Mycomicrothelia apposita** (Nyl.) D. Hawksw., **comb. nov.**

Verrucaria apposita Nyl. in *Annls Sci. nat., Bot.* IV, **20**: 254 (1863).
Arthopyrenia apposita (Nyl.) H. Olivier, *Exp. Lich. Ouest Fr.* **2**: 258 (1902).
Microthelia apposita (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).

Fig. 9A–D.

Ascomata arising singly or more rarely becoming confluent at the edges, scattered over whitish areas of bark, colonies well-marked but not with a marginal black line, immersed, subepidermal, the epidermal layers raised to form hemispherical projections; individual ascomata dimidiate, applanate but not strongly so, (300–)350–450(–500) μm diam, mainly 150–200 μm tall, basal fringe not apparent; ostiole depressed, conspicuous, whitish within, mainly 70–100 μm diam; involucrellum dark reddish brown, ± unchanged in potassium hydroxide, well-developed, 40–80 μm thick, consisting of host tissue intermixed with hyphae, hyphae 2·5–3·5 μm thick, red brown, uneven, smooth-walled, entering the host cells as well as ramifying amongst them; basal tissue scarcely differentiated from the generative tissues, subhyaline; exciple subhyaline to pale brown hyphae forming a layer mainly 10–15 μm thick but becoming darker in colour and thicker in the ostiolar region; centrum not turning blue in iodine. *Pseudoparaphyses* persistent, probably cellular, numerous, occasionally septate, branched and anastomosing, mainly 2–3·5 μm wide. *Asci* arising from the tissue lining the base of the ascomata, ± vertically arranged inclined towards the ostiole, subcylindrical, with a distinct stalk, bitunicate, with a clear internal apical beak, 90–120 × 14–16 μm, 8-spored. *Ascospores* ± uniseriately arranged in the asci but overlapping to a slight extent, sometimes almost distichously arranged, ellipsoid, 1-septate, occasionally with 2 pseudosepta, only slightly constricted at the septum, the lower cell slightly smaller, apices distinctly attenuated, a germ pore evidently developing at the apices, reddish brown, rather coarsely verruculose, with a very thin gelatinous sheath (to 1 μm thick in potassium hydroxide), (22–)24–28(–29·5) × (8·5–)9–11·5(–12·5) μm.

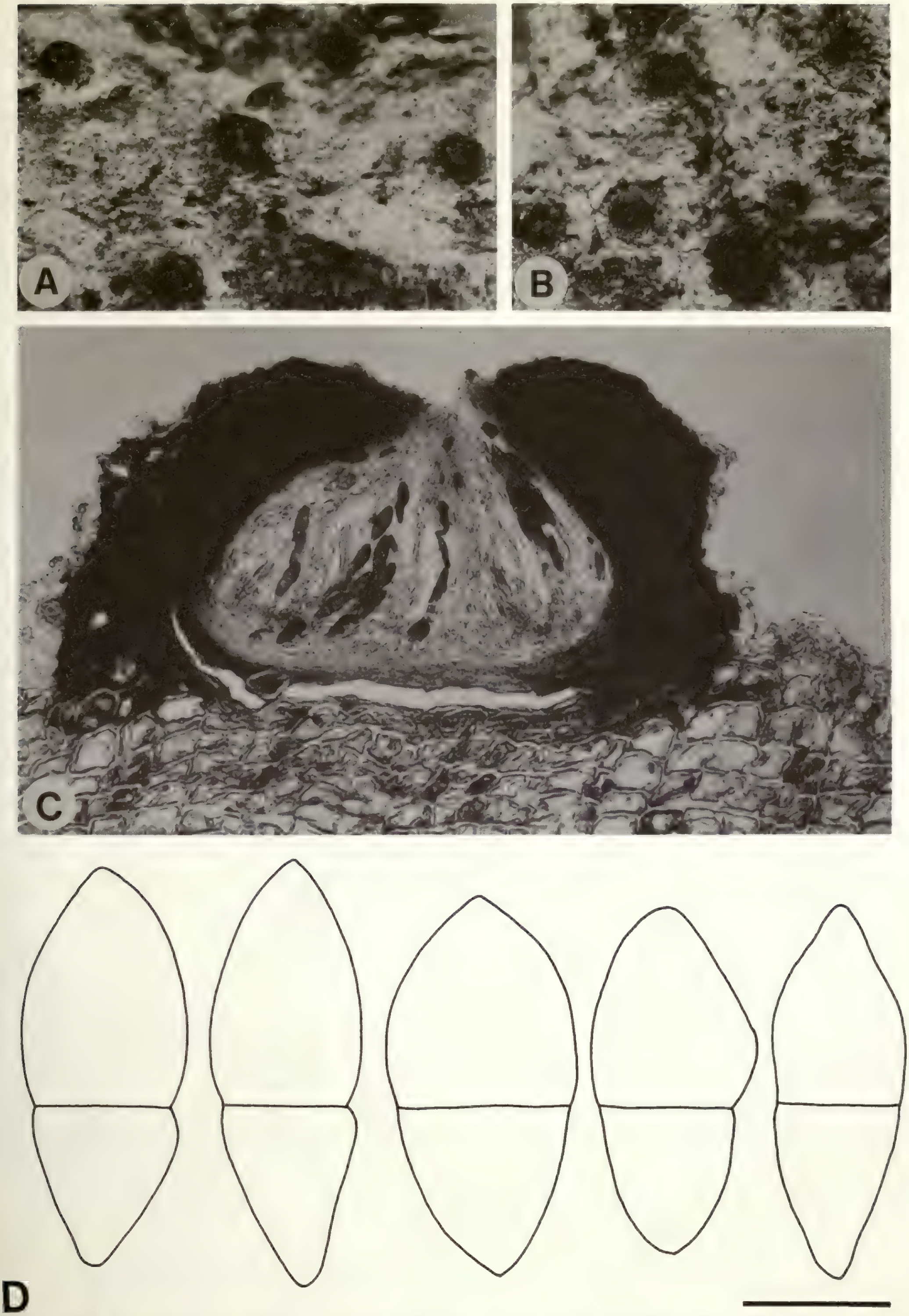

Fig. 9 *Mycomicrothelia apposita* (**A–B**, **D** H-NYL 702—holotype; **C** H-NYL p.m. 6481—isotype). **A–B**, Surface view, × 20. **C**, Vertical section of ascoma, × 250. **D**, Ascospore outlines, scale = 10 μm.

Anamorph: Unknown.

Host: Unidentified bark. Probably lichenized with *Trentepohlia*.

Distribution: Colombia. Known only from the original collection.

Observations: This species recalls *Mycomicrothelia thelena* in the large ascospores and rich development of almost trabeculate-like pseudoparaphyses. The two taxa are, however, clearly separable on the basis of both the shape of the asci and the pointed apices of the ascospores of *M. apposita*.

Three collections of this species are present in H-NYL and a further one was discovered in M. The one in H-NYL bearing Nylander's descriptive notes is regarded as the holotype and the remaining collections as isotypes. The spelling *'adposita'* appears on two packets.

Specimens: **Colombia:** ['Nova Granata, Choachi (Paramo)'], 3500 m, 'as ramos arbustorum', *A. Lindig* 815 (H-NYL 702—holotype; H-NYL 707, H-NYL p.m. 7481, M—isotypes).

3. **Mycomicrothelia atlantica** D. Hawksw. & Coppins, **sp. nov.**

Ascomata perithecia, immersa, dimidiata, nigra, (150–)200–300(–350) μm lata, 90–120 μm alta; muris 20–35 μm latis, textura intricata, atrobrunneis; centrum pro parte cum iodo violescens. Paraphyses (pseudoparaphyses) persistentes, ramosae et anastomosantes, septatae, 1·5–2·5 μm latae. Asci bitunicati, clavati, 40–55 × 12–17 μm, 8-spori. Ascosporae distichae in asco, ellipsoideae, 1-septatae, olivaceobrunneae, verruculosae, (12·5–)13·5–16(–17·5) × (5·5–)6·5–8(–9) μm. Conidiomata pycnidia, 45–75 μm diam; cellulae conidiogenae phialidicae, 3–6 × 2–3 μm; conidia bacilliformia, hyalina, 3–4 × 0·5–0·7 μm.

Typus: Magna Britannica, Scotia: Westerness (V.C. 97), south side of Loch Sunart, Laudale Woods, on *Corylus*, 9 March 1983, *B. J. Coppins & P. M. Jørgensen* 9344 (IMI 291259—holotypus; BM, E—isotypi).

Figs 10A–F, 11A–E.

Ascomata arising singly, occasionally 1–2 adpressed, scattered on scarcely unchanged brownish portions of the bark, colonies not delimited by a marginal line, immersed, the outer peridermal layers slightly raised as low punctiform projections; individual ascomata dimidiate, (150–)200–300(–350) μm diam, 90–120 μm tall, black, shiny, with a purplish-black basal fringe extending for 30–50 μm around the ascomata, ostiole depressed; involucrellum dark reddish brown, becoming olivaceous in potassium hydroxide, 20–35 μm thick, consisting of periderm cells intermixed with fungal hyphae, hyphae irregularly orientated, 1·5–2·5 μm thick, uneven in diameter, sometimes penetrating the host cells which become somewhat occluded; exciple mainly 5–12 μm thick, composed of a few irregular layers of brown interwoven and compressed hyphae (textura intricata); base composed of similar hyphae to the exciple sides but often poorly developed, almost absent to *c.* 7 μm thick; centrum when young in parts turning pale violet (not blue) in iodine (following treatment in potassium hydroxide). *Pseudoparaphyses* cellular, persistent, branched and anastomosing, septate, 1·5–2·5 μm thick. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated, clavate, bitunicate, strongly thickened apically, with an internal apical beak, short-stalked, 40–55 × 12–17 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, 1-septate, not or slightly constricted at the septum, cells ± equal in size, apices rounded, olivaceous, verruculose, with a thin gelatinous sheath 1–1·5 μm thick in potassium hydroxide, (12·5–)13·5–16(–17·5) × (5·5–)6·5–8(–9) μm.

Anamorph: Pycnidia immersed, arising between the ascomata, 45–75 μm diam, brownish-black, ostiole depressed, to 30 μm diam; walls irregularly pseudoparenchymatous, sometimes extended around the ostiole into a clypeate involucrellum, mainly 3–7 μm thick, cells mainly 2–3 μm diam. *Conidiogenous* cells simple, hyaline, elongate-ampulliform, phialidic, 3–6 × 2–3 μm. *Conidia* bacillariform, hyaline, 3–4 × 0·5–0·7 μm.

Host: On smooth bark of *Corylus avellana*, often growing in deep shade. Sometimes loosely associated with *Trentepohlia* but probably not lichenized.

Distribution: British Isles. Known only from western Scotland and south-west Ireland.

Observations: This new species is probably most closely related to *Mycomicrothelia macularis*, which has similar pycnidia and conidia, but can be separated from that species by the broader ascospores, which are not so markedly constricted centrally, and the smaller ascomatal fringe. *M. confusa*, which also occurs on *Corylus*, has a creamy or whitish thallus, usually delimited by a

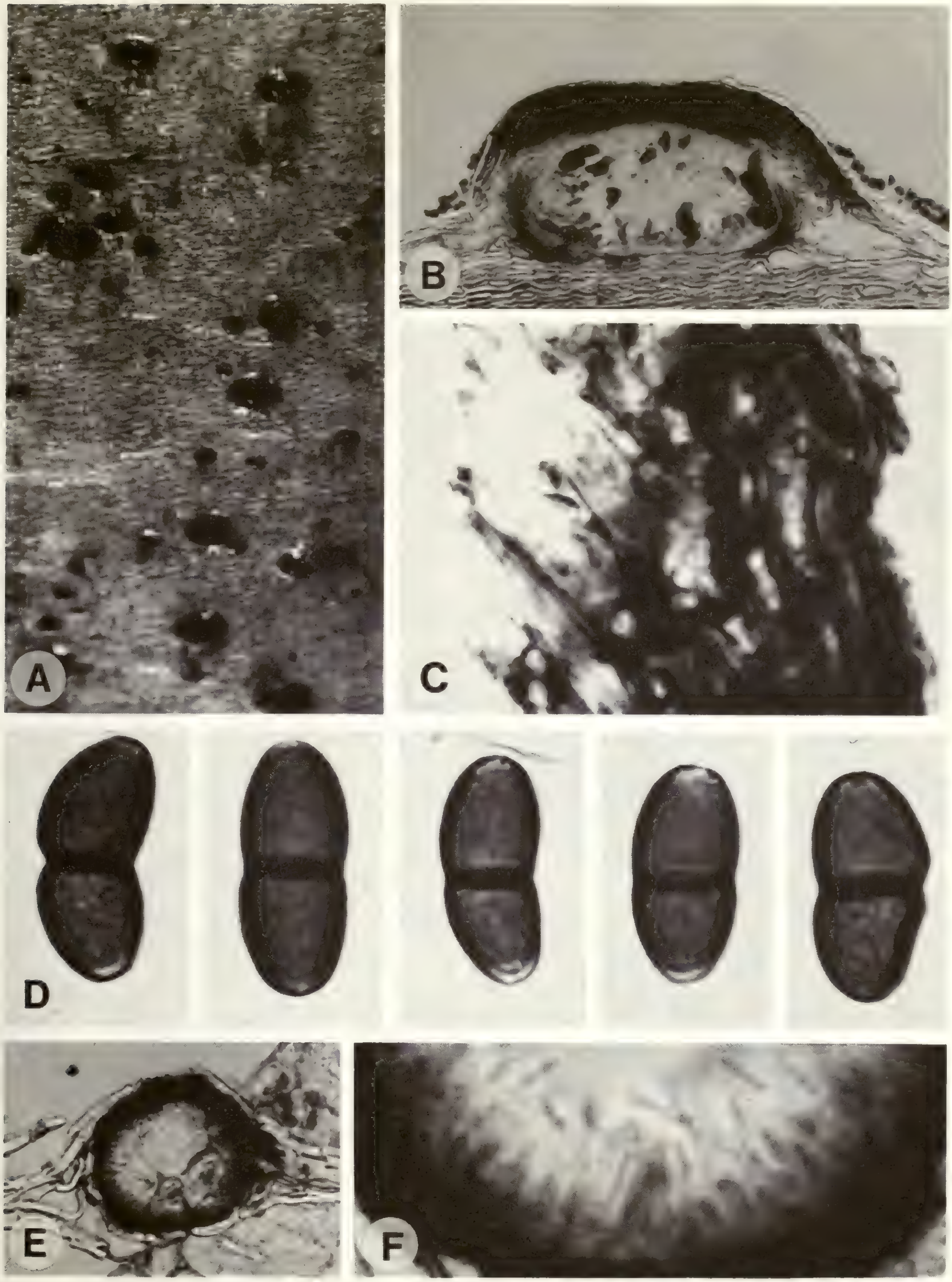

Fig. 10 *Mycomicrothelia atlantica* (IMI 291259—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 200. **C**, Detail of exciple structure showing hyphal structure, × 2200. **D**, Ascospores, × 2200. **E**, Vertical section of conidioma, × 200. **F**, Detail of conidioma showing conidiogenous cells and conidia, × 2200.

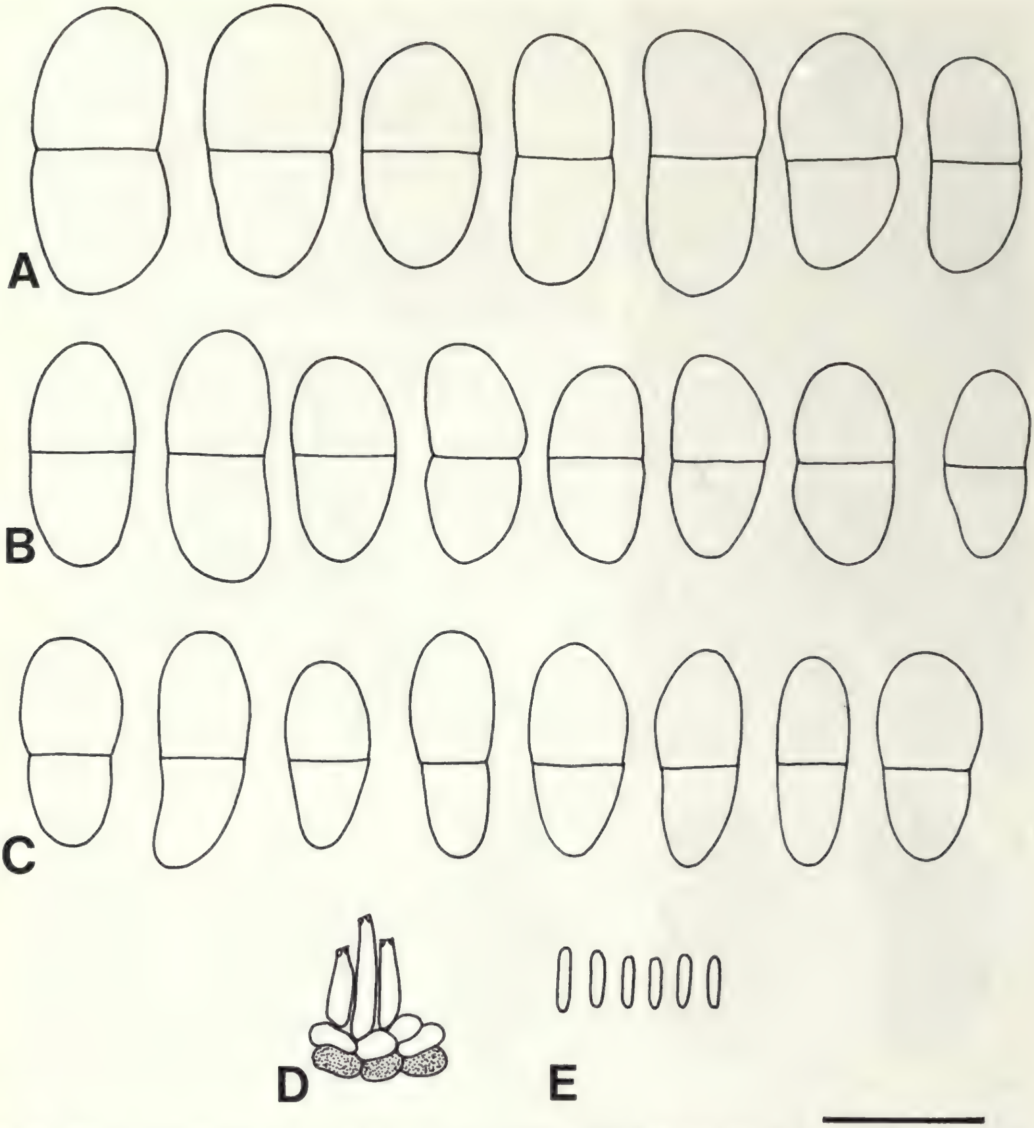

Fig. 11 *Mycomicrothelia atlantica* **A–C**, Ascospore outlines; **A**, IMI 291259—holotype; **B**, Torc Mountain, *P. W. James*, BM; **C**, IMI 126822. **D–E**, Conidiogenous cells and conidia (IMI 291259—holotype). Scale = 10 μm.

black line, longer ascospores which generally have unequal and attenuated rather than smoothly rounded cells, no pycnidia, and does not give any reaction with iodine. Pycnidia are well-represented on all three collections seen, and appear to be a useful field criterion for the separation of *M. atlantica* from *M. confusa*; the small size of the conidia suggests that they may be spermatial in function rather than diaspores.

Specimens: **British Isles:** Scotland, Westerness, south side of Loch Sunart, Laudale Woods, on uppermost part of *Corylus* stems, 9 March 1983, *B. J. Coppins & P. M. Jørgensen* 9344 (IMI 291259—holotype; BM, E—isotypes); north side of Loch Sunart, Resipole Ravine, on *Corylus*, 10 March 1983, *B. J. Coppins & P. M. Jørgensen* 9429 (E). Ireland: Co. Clare, The Burren, on *Corylus avellana*, March 1967, *C. H. Dickinson* (IMI 126822); Co. Kerry, Killarney, Torc Mountain, on *Corylus*, 28 February 1965, *P. W. James* (BM).

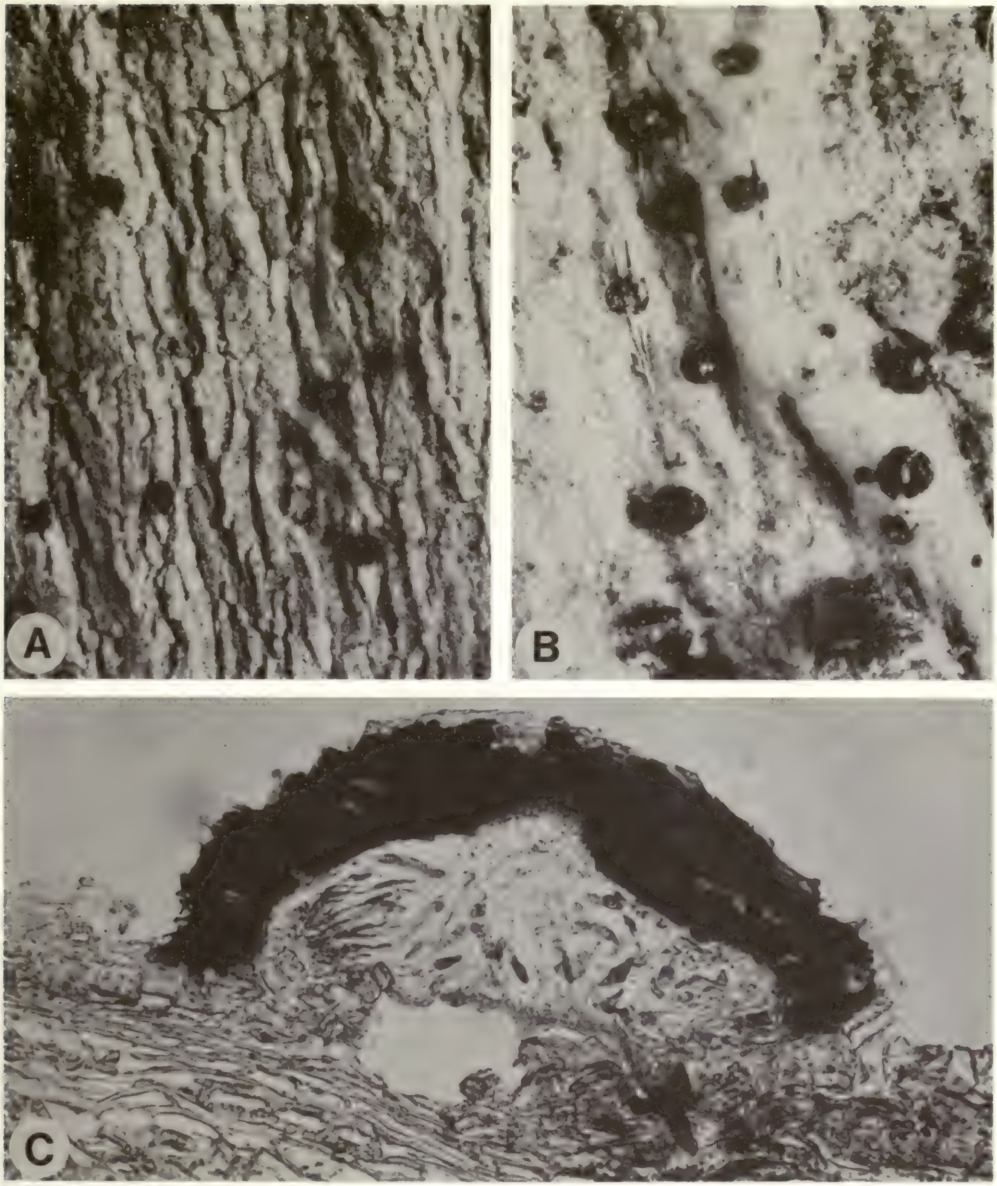

Fig. 12 *Mycomicrothelia captiosa*. **A**, Surface view (M—lectotype of *Verrucaria captiosa*), × 20. **B**, Surface view (G—holotype of *Microthelia flavicans*), × 20. **C**, Vertical section of ascoma (*Glaziou* 5057b, M), × 250.

4. Mycomicrothelia captiosa (Krempelh.) D. Hawksw., **comb. nov.**

Verrucaria captiosa Krempelh. in *Flora, Jena* **59**: 524 (1876).
Microthelia captiosa (Krempelh.) Müll. Arg. in *Bot. Jb.* **6**: 416 (1885).
Microthelia flavicans Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **32**: 170 (1894).

Figs 12A–C, 13A–C.

Ascomata arising singly, scattered, colonies whitish-rose, delimited by a black line, immersed, subepidermal, the epidermis raised to form low hemispherical projections; individual ascomata dimidiate, applanate, (200–)250–350(–400) μm diam, 150–225 μm tall, basal fringe poorly developed and mainly 25–40 μm wide, ostiole depressed, to 60 μm diam, black; involucrellum very dark reddish brown to almost black, slightly olivaceous in potassium hydroxide, 50–65 μm thick, consisting of host tissue interspersed with fungal hyphae, hyphae 2·5–3·5 μm thick, red brown, uneven, smooth-walled; basal tissue of the ascomata subhyaline and indistinguishable from the generative locule; exciple a few layers of pale brown interwoven hyphae 2–3 μm diam forming a layer to 15 μm thick near the ostiole, not continued below the locule; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, filiform, branched and anastomosing, 1·5–2·5 μm thick. *Asci* arising mainly from the angles of the ascomata and inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a small internal apical beak, (55–)65–73 × (12–)13–14 μm, 8-spored. *Ascospores* distichously arranged in the

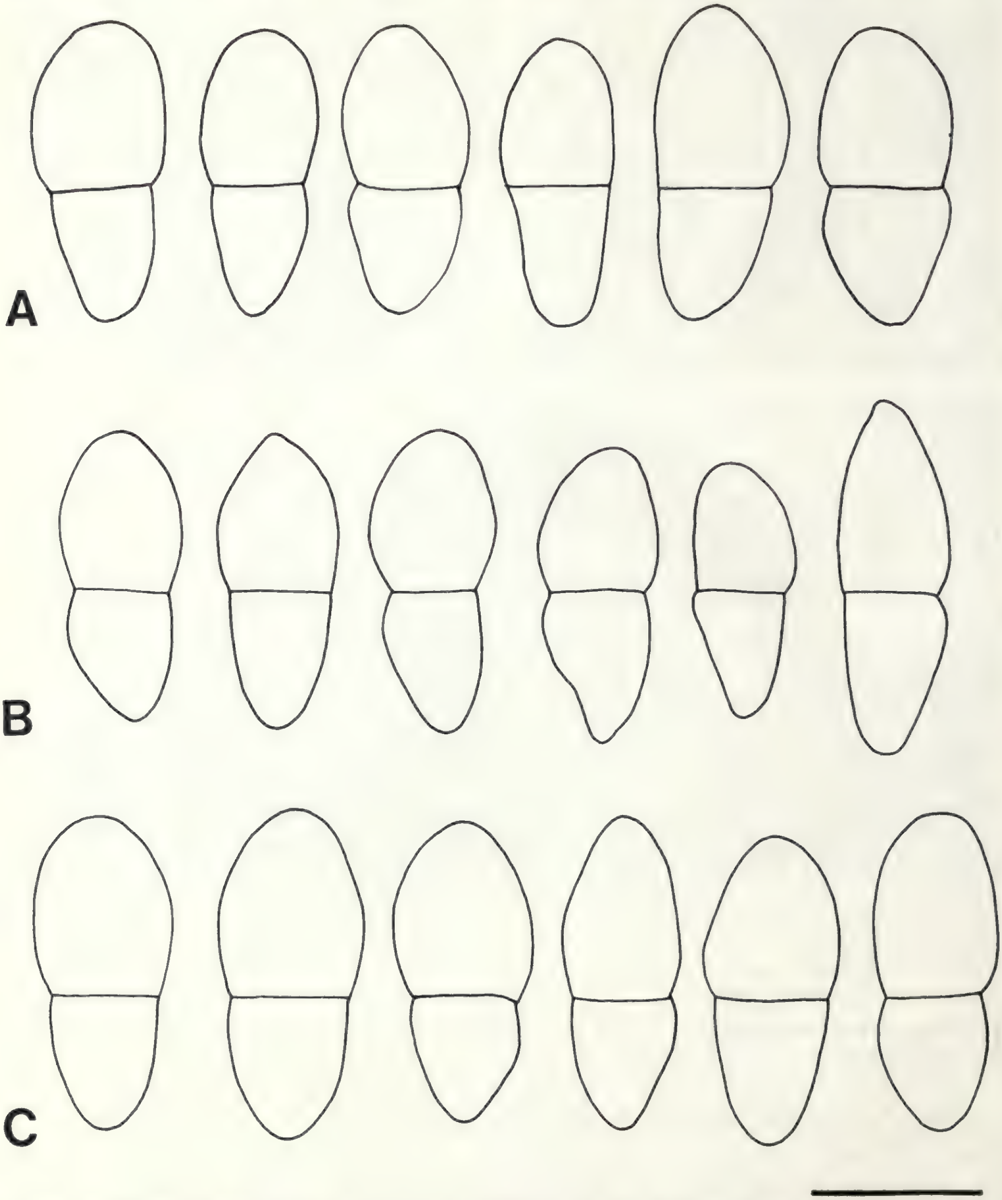

Fig. 13 *Mycomicrothelia captiosa* ascospore outlines. **A**, M—lectotype of *Verrucaria captiosa*. **B**, G—holotype of *Microthelia flavicans*. **C**, G—syntype of *M. intercedens*. Scale = 10 μm.

asci, ellipsoid to somewhat soleiform, 1-septate, slightly constricted at the septum, the upper cell slightly larger, apices rounded to slightly attenuated, olivaceous brown, verruculose, with a thin gelatinous sheath to 1·5 μm thick in potassium hydroxide, (13·5–)17–19(–21) × (5·5–)6·5–7·5 (–8·5) μm.

Anamorph: Unknown.

Host: Unidentified bark. Apparently lichenized, presumably with *Trentepohlia*.

Distribution: Brazil and Costa Rica.

Observations: This species is rather close to *Mycomicrothelia socialis* in its microscopical features but is separated from that species in that the ascomata are not aggregated into small groups, the better delimited colonies, and narrower asci.

Three specimens were mentioned in the original account of the species; that including notes of the characters of the species is selected here as the lectotype.

In the San José collection the spores tend to be in the upper range of the species, with many over 18 μm, while in the lectotype they only rarely exceed 18 μm.

In the holotype of *Microthelia flavicans* the thallus has a pale greenish-yellow tinge, but is evidently moribund and old as many of the ascomata are effete; the ascomata sectioned were to only 160 μm tall, but similar in diameter. However, the thallus has a delimiting black line, and the ascospores measured (15–)17–19(–21) × 7–7·5(–8) μm. It therefore seems clear that these taxa should be united.

Specimens: **Brazil:** Rio de Janeiro, *A. Glaziou* 5057a (M—lectotype of *Verrucaria captiosa*), 5057b (M), 5023b (M). – **Costa Rica:** San José, Tondaz, 1893, *H. Pittier* (G—syntype of *Microthelia intercedens:* see p. 90); Tondaz, 1893, *H. Pittier* 6307 (G—holotype of *Microthelia flavicans*).

5. **Mycomicrothelia confluens** (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia confluens Müll. Arg. in *Flora, Jena* **68**: 333 (1885).

Verrucaria confluens (Müll. Arg.) Stizenb. in *Ber. Tät. St. Gall. naturw. Ges.* **1889/90**: 217 (1891), nom. illegit. (Art. 64.1), non *V. confluens* (Weber) Hoffm., *Descr. Pl. Lich.* **1**: 87 (1790).

Figs 14A–B, 15.

Ascomata arising in groups of 2–8 united by a common fringe, often tending to be orientated in lines, occasionally arising singly, scattered over the bark surface which is scarcely discoloured, margins of colonies not seen, immersed, subepidermal, the outer layers raised to form plateaux with hemispherical projections, black; individual ascomata dimidiate, strongly compressed with an applanate base, (250–)300–400(–500) μm diam, 120–170 μm tall, basal fringe wide-spreading, extremely well-developed and 200–400 μm wide uniting several ascomata and causing the level of the bark to be raised, ostiole depressed, visible as a whitish spot; involucrellum dark reddish brown but becoming distinctly olivaceous in potassium hydroxide, very thick and mainly 60–100 μm, extending well beyond the limits of the ascomatal cavity, composed of 10–15 layers of host cells intermixed with fungal hyphae, the hyphae radiating, reddish brown but distinctly olivaceous in potassium hydroxide, even above the ascomata where they are arranged almost parallel to each other but becoming less regular in the basal fringe, smooth-walled, mainly 2–3 μm thick; basal tissue not differentiated from the generative tissues; hyaline; exciple composed of interwoven hyphae similar to those of the involucrellum and fringe but more compacted and forming a layer which reaches about 15 μm thick near the ostiole but is poorly developed below; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, filiform, repeatedly septate, branched and anastomosing, 2–3(–3·5) μm thick. *Asci* in the mature state not seen, young asci elongate-clavate and evidently bitunicate with a distinct internal apical beak, arising centrally and in the angles of the ascomatal cavity, orientated towards the ostiole. *Ascospores* ellipsoid, 1-septate, slightly constricted at the septum, the upper cell usually slightly larger, apices somewhat attenuated to rounded, golden brown, distinctly verruculose, with a thin gelatinous sheath 1–2 μm thick in potassium hydroxide, (21–)22–25 × 7·5–9(–10·5) μm.

Anamorph: Unknown.

Host: Unidentified bark. Probably not lichenized.

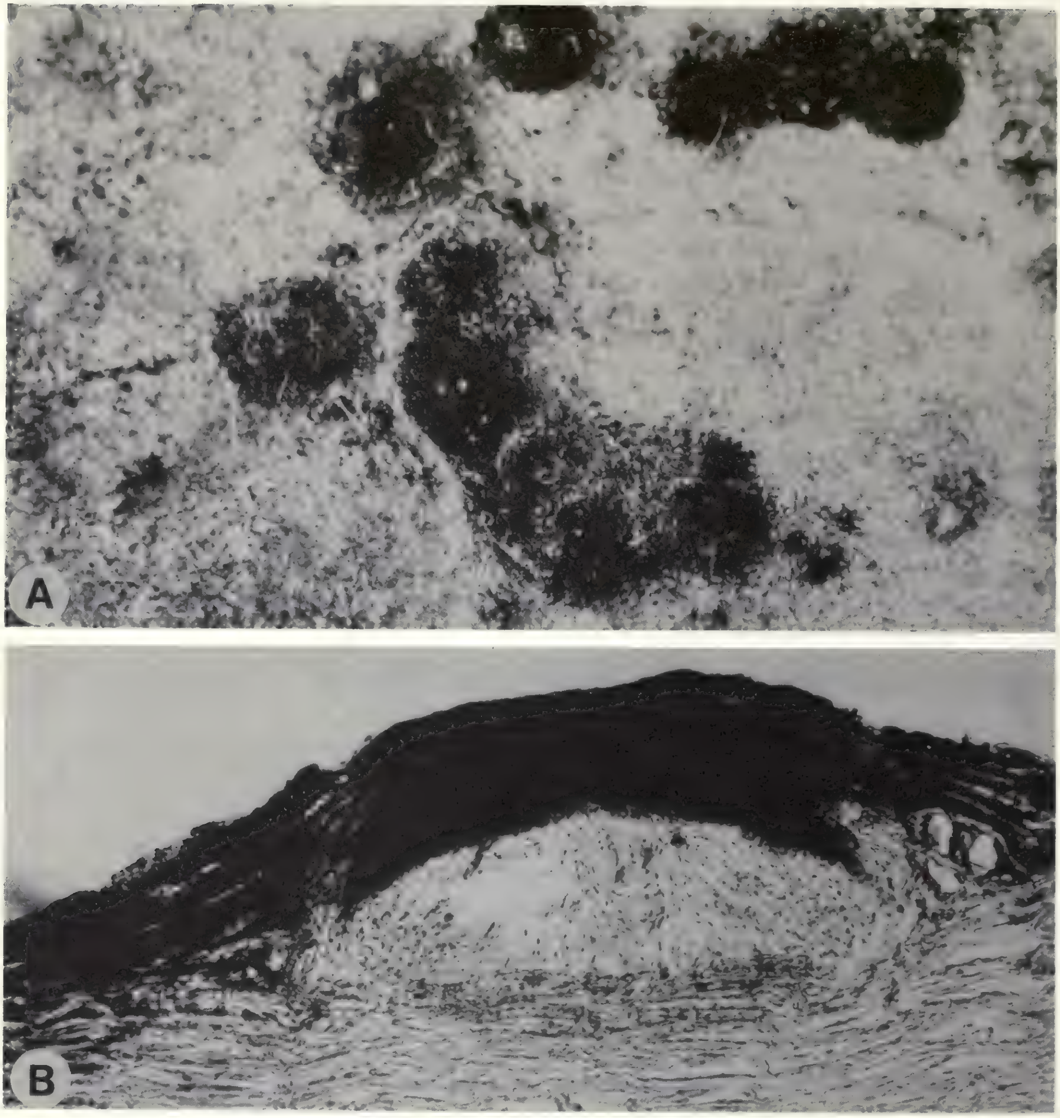

Fig. 14 *Mycomicrothelia confluens* (G—holotype). **A**, Surface view showing ascomata united by a common fringe, × 20. **B**, Vertical section of ascoma, × 250.

Distribution: South Africa. Known only from the original collection.

Observations: This species recalls *Mycomicrothelia thelena* in the length of the ascospores, but these are rather narrower than is typical for that species. More importantly, the ascomata in *M. confluens* arise deeply within the bark and have an extremely well-developed basal fringe which unites several ascomata together into single plateaux scattered over the bark surface. The whitish thallus characteristic of *M. thelena* is also lacking in *M. confluens*.

No additional material of this species was located in VER (V. A. Bianchini, in litt.).

Specimen: **South Africa:** Cape of Good Hope, 'ex hb. Hampe 1877' (G—holotype).

6. **Mycomicrothelia confusa** D. Hawksw., **sp. nov.**

Ascomata perithecia, immersa, dimidiata, nigra, 200–300(–400) μm lata, 90–125 μm alta; muris 25–40 μm latis, textura intricata ex hyphis atrobrunneis et cellulis hospitis; centrum cum iodo non reagens.

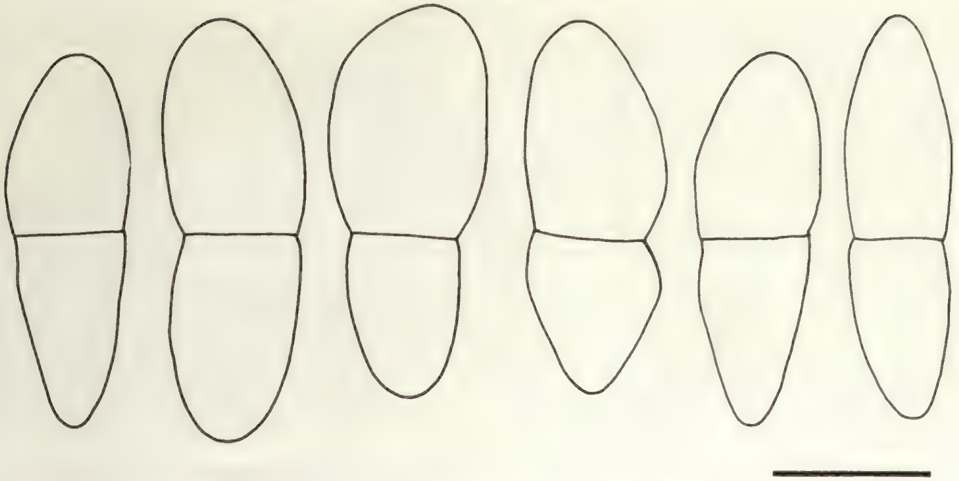

Fig. 15 *Mycomicrothelia confluens* ascospore outlines (G—holotype). Scale = 10 μm.

Paraphyses (pseudoparaphyses) persistentes, ramosae et anastomosantes, septatae, 1·5–2 μm latae. Asci bitunicati, elongato-clavati, 55–70 × 12–18 μm, 8-spori. Ascosporae distichae in asco, soleiformes, 1-septatae, olivaceo-brunneae, verruculosae, (15·5–)17·5–21(–25) × (6–)7–9(–10) μm.

Typus: Magna Britannica, Scotia: Mid-Ebudes (V.C. 103), Mull, Kellan Mill, on *Corylus* in small ravine, 13 May 1968, *P. W. James* (BM—holotypus).

Figs 16A–D, 17A–F, 18A–D.

Ascomata arising singly, rarely confluent, scattered on creamy or whitish patches of bark, sharply delimited only where juxtaposed to other species, a purplish-black marginal line to 50 μm wide then sometimes develops, immersed, the outer peridermal layers raised to form low hemispherical projections; individual ascomata dimidiate, 200–300(–400) μm diam, 90–125 μm tall, black, shiny, basal fringe poorly developed and rarely extending more than 25 μm, ostiole depressed or ± plane; involucrellum dark reddish brown, becoming olivaceous green in potassium hydroxide, 25–40 μm thick, consisting of periderm cells intermixed with fungal hyphae, hyphae irregularly orientated, 2·5–3·5 μm thick, uneven in diameter, penetrating the periderm cells the lumina of which can become completely occluded; exciple 10–15 μm thick, composed of a few irregular layers of brown, often unevenly thickened hyphae (textura intricata); base of ascoma similar in structure to the upper parts of the ascomata, very variable in development, uneven, ± absent to 20 μm thick; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, branched and anastomosing, septate, 1·5–2 μm thick. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated or inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with an internal apical beak, 55–70 × 12–18 μm, 8-spored. *Ascospores* distichously arranged in the asci, soleiform, 1-septate, constricted at the septum, the lower cell usually narrower but either shorter to longer than the upper, the upper cell generally rounded, the lower generally attenuated and sometimes constricted along its length, olivaceous brown, often guttulate (fresh material), delicately verruculose, with a thin gelatinous sheath swelling to 2 μm (exceptionally more) in potassium hydroxide, (15·5–)17·5–21(–25) × (6–)7–9(–10) μm.

Anamorph: Unknown.

Hosts: Smooth bark, especially *Corylus avellana*, but also known from *Betula, Fraxinus excelsior, Ilex aquifolium, Quercus,* and *Sorbus aucuparia*. Almost always in shaded and ± constantly humid situations. Rather loosely associated with algae, facultatively lichenized with *Trentepohlia*.

Distribution: British Isles and Norway, with a pronounced Atlantic distribution, but to be expected elsewhere along the Atlantic seaboard of Europe.

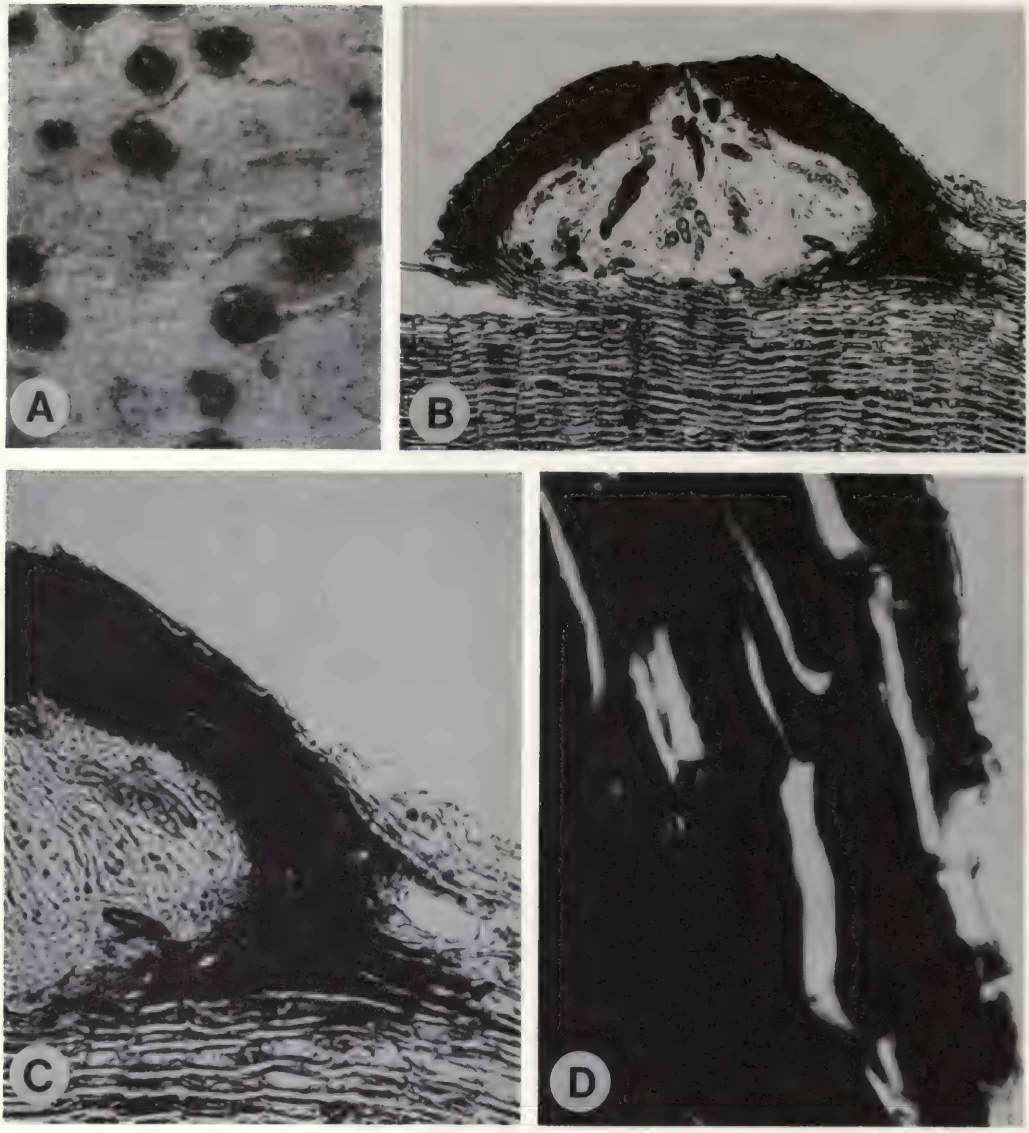

Fig. 16 *Mycomicrothelia confusa* (BM—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 200. **C**, Vertical section of portion of ascoma, × 400. **D**, Detail of structure of involucrellum showing clypeate tissue formed of fungal hyphae and cells from the host periderm, × 2200.

Observations: This is the species to which the name *'Microthelia micula'* has been most commonly applied by British authors, although most reports from lowland Britain refer to *Kirschsteiniothelia aethiops* (see Hawksworth, 1985*a*). Continental European references to *'M. micula'* mainly refer to *Peridiothelia fuliguncta* (see p. 121).

Mycomicrothelia confusa forms distinctive creamy or whitish patches on the bark which are a useful field character for the separation of this species from *M. atlantica*, which also occurs on *Corylus*; the separation of these two species is discussed in further detail above (see p. 70).

The ascospore shape in *M. confusa* is particularly distinctive in the genus, with the lower cell at least becoming attenuated and somewhat constricted along its length. This feature, together with the ascospore dimensions, readily separates this taxon from other species of *Mycomicrothelia*.

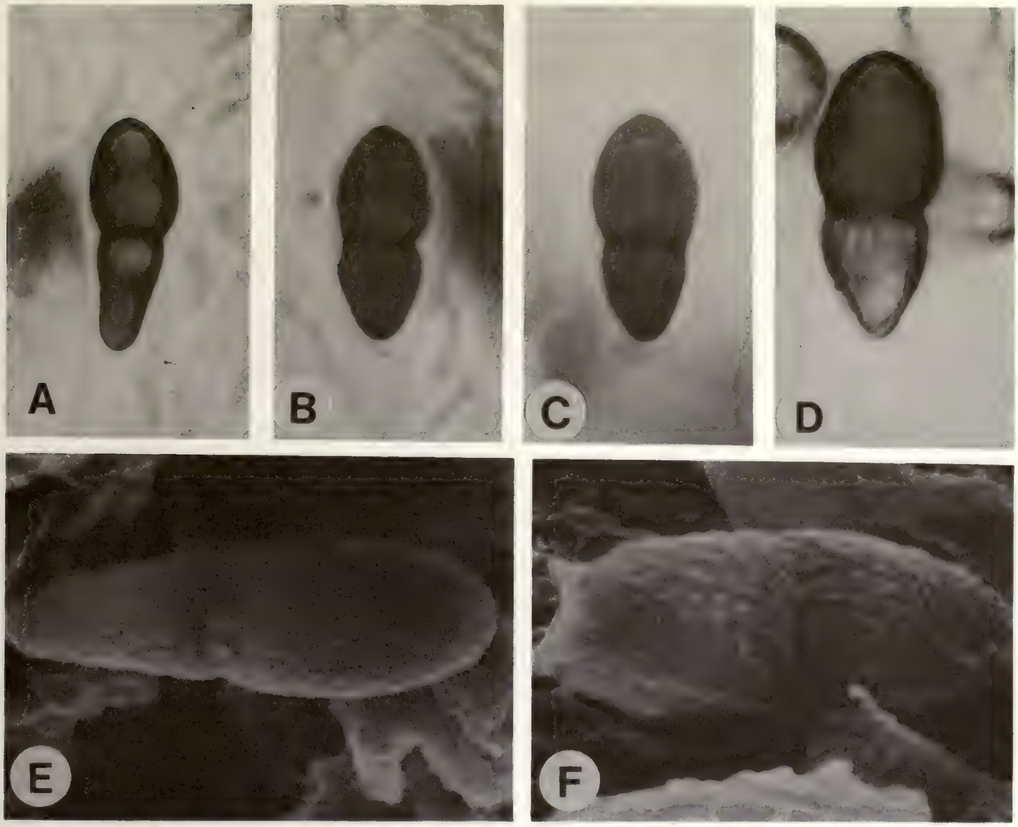

Fig. 17 *Mycomicrothelia confusa* (BM—holotype). **A–C**, Ascospores, × 1600. **D**, Ascospore showing ornamentation, × 2200. **E–F**, Scanning electron micrographs of ascospores; **E**, × 5500, **F** × 6000.

Specimens: **British Isles:** ENGLAND: South Devon, Ivybridge, *E. M. Holmes* (BM); Kingsbridge, Slapton Ley Nature Reserve, France Wood, on *Quercus*, 7 August 1970, *D. L. Hawksworth & K. L. Alvin* 2382*a* (IMI 152971*a*). – SCOTLAND: Argyllshire, Glasdrum National Nature Reserve, on *Corylus*, 27 May 1976, *B. J. Coppins* 1824 (E); Glen Nant National Nature Reserve, Tailor's Leap, on *Quercus* twigs, 28 May 1976, *B. J. Coppins* 2687 (E); Seil, Ballachuan hazel woods, on *Corylus*, 30 June 1976, *B. J. Coppins* 2555 (E); north side of Loch Etive, wood by Blarcreen Burn, on *Sorbus*, 7 August 1980, *B. J. Coppins* 8090 (E); Cowal Peninsula, Upper Glen Shira, Drimlee, on *Corylus*, 25 June 1977, *P. W. James* (BM); Cowal Peninsula, Glendaruel Forest, on *Corylus*, 28 June 1977, *P. W. James* (BM). Kintyre, Ellary Woods, south of Loch Meadhonach, on *Quercus*, 2 July 1976, *B. J. Coppins* 2641 (E). South Ebudes, Colonsay, Coille Mhór, on *Corylus*, 27 August 1981, *B. J. Coppins* 8673 (E). Mid-Ebudes, Coll, west side of Loch Fada, on *Sorbus*, April 1983, *B. J. Coppins* 9601 (E); Coll, south-west of Bousd, on *Corylus* in gulley, 17 April 1983, *B. J. Coppins* 9647 (E); Mull, 1 mile east of Achronich opposite Eorsa, on *Fraxinus*, 11 May 1968, *P. W. James* (BM); Mull, Tobermoray, Aros Woods, on *Corylus*, 3 July 1966, *P. W. James* (BM); Mull, An Coire Wood, on *Corylus*, 12 September 1967, *P. W. James* (BM); Mull, Alterich, Scallastle Bay, on *Betula*, 10 May 1968, *P. W. James* (BM); Mull, Kellan Mill, on *Corylus*, 13 May 1968, *P. W. James* (BM—holotype). Westerness, Morven, Killudine River, on *Corylus*, 1 July 1962, *P. W. James* (BM); Cona Glen pinewood, on *Sorbus*, 30 May 1975, *B. J. Coppins* 2303 (E); Knoydart, between Stob na Muicraidh and Bachd Mhic an Tosaich, on *Corylus*, 22 May 1975, *B. J. Coppins* 2201 (E); north side of Loch Sunart, Camasine, on *Fraxinus*, *B. J. Coppins* 9232 (E, IMI 291558); south side of Loch Sunart, Laudale Woods, on *Corylus*, 9 March 1983, *B. J. Coppins* 9368 (E). – IRELAND: Co. Kerry, by Loch Inchiquin, August 1864, *I. Carroll* (BM); Gleucar, August 1864, *I. Carroll* (BM); Killarney, Mangerton, September 1867, *I. Carroll* (BM); Killarney, *H. Piggot* (BM), Turk Mt., June 1877, *I. Carroll* (BM), Croghaue, April 1867, *I. Carroll* (BM); Old Dromore, August 1864, *I. Carroll* (BM); Killarney, Muckross Woods, on *Betula*, March 1856, *I. Carroll* (E), on *Ilex*, 14 August 1966, *P. W. James* (BM). Co. Cork, Glengarriff, on *Ilex*, March 1858, *I.*

Carroll (BM, E). Co. Galway, Derryclare Wood, 7 August 1966, *G. Morgan-Jones* (IMI 190767*a*); Connemara, Ballynahinch, on *Corylus*, 2 March 1965, *P. W. James* (BM). – **Norway:** In Seilandeh ad Storvandel, Gyfjord, on *Sorbus, J. M. Norman* (O).

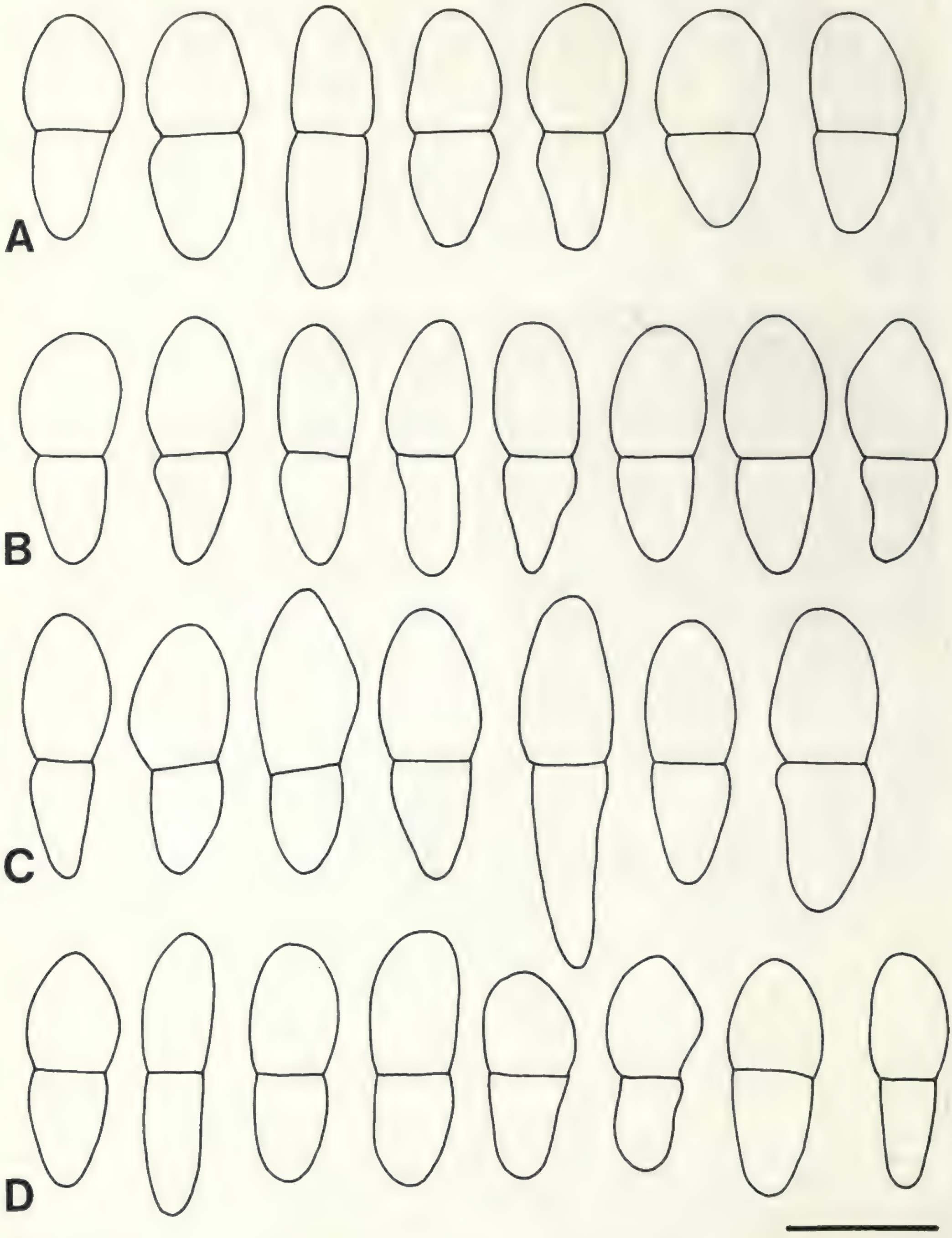

Fig. 18 *Mycomicrothelia confusa* ascospore outlines. **A**, BM—holotype. **B**, On *Quercus*, IMI 190767a. **C**, On *Corylus*, 28 June 1979, *P. W. James*, BM. **D**, On *Sorbus, J. M. Norman*, O. Scale = 10 μm.

7. Mycomicrothelia conothelena (Nyl.) D. Hawksw., **comb. nov.**

Verrucaria conothelena Nyl. in *Bull. Soc. linn. Normandie* II, **7**: 180 (1873).
Microthelia conothelena (Nyl.) Zahlbr., *Cat. Lich. Univ.* **1**: 258 (1921).
Verrucaria conothelena var. *errans* Nyl. in *Bull. Soc. linn Normandie* II, **7**: 180 (1873).
Microthelia conothelena var. *errans* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **1**: 258 (1921).

Fig. 19A–C.

Ascomata arising singly, scattered, on a pale brownish thallus, colonies delimited by a black band to 75 μm broad, erumpent, hemispherical to almost mammiform; individual ascomata dimidiate, (250–)300–400(–450) μm diam, 200–250 μm tall when mature, no distinct basal fringe developed, black; involucellum dark brown, becoming somewhat more olivaceous in potassium hydroxide, mainly 30–50 μm thick but to 70 μm on the lower sides, composed of numerous irregular layers of interwoven hyphae, also including host cells in the lower parts of the sides and

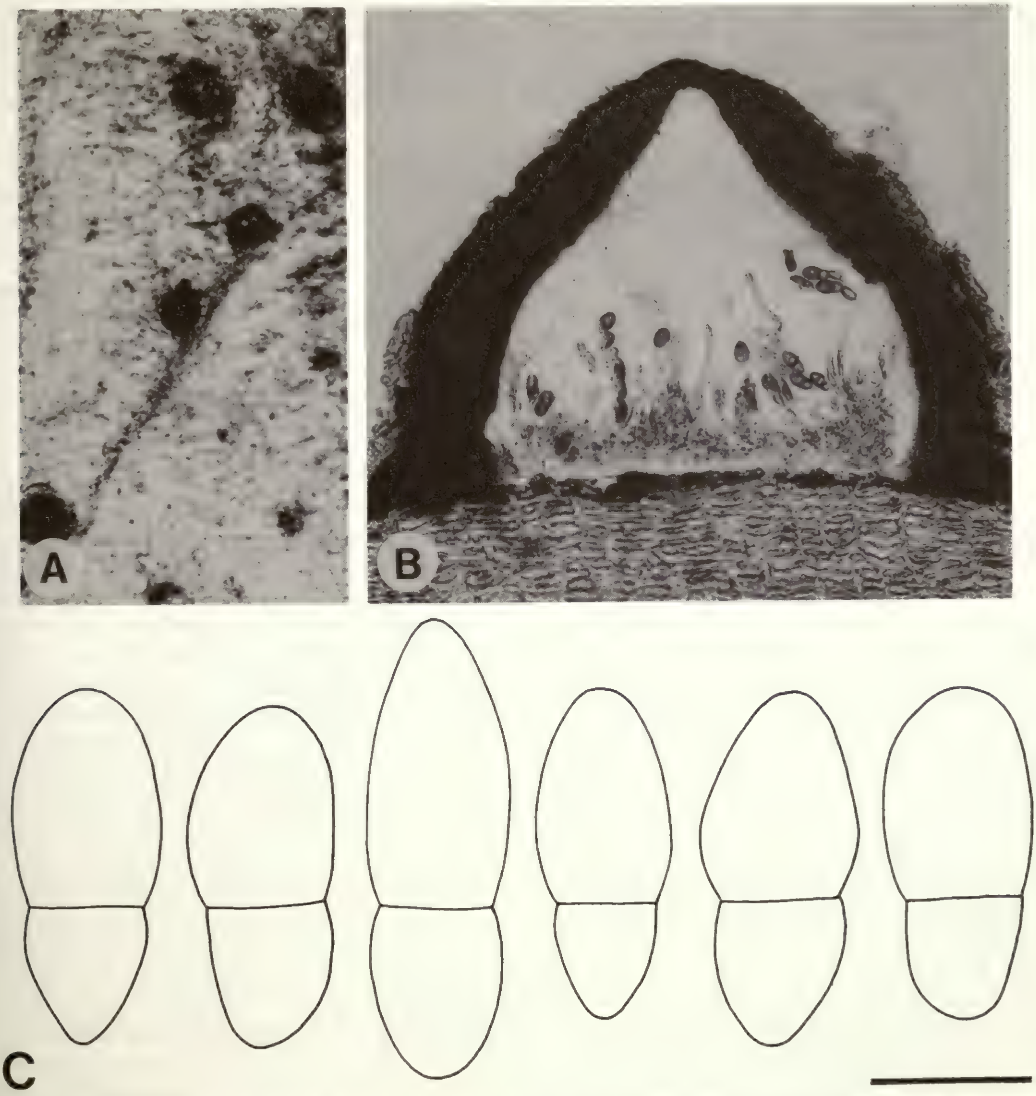

Fig. 19 *Mycomicrothelia conothelena.* **A**, Surface view (H-NYL 704—lectotype), × 20. **B**, Vertical section of ascoma (M—isolectotype). **C**, Ascospore outlines (M—isolectotype), scale = 10 μm.

scattered in the upper parts of the cone, hyphae reddish brown, mainly 1·5–2·5 μm thick, uneven, ± smooth-walled; exciple poorly differentiated from the involucrellum, similar in structure but paler brown; basal tissue reduced to irregular brownish hyphae intermixed with the periderm cells of the host, the generative tissue often abutting directly onto the host cells; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, abundant, persistent, branched and anastomosing, (1·5–)2–2·5 μm thick. *Asci* arising from the base of the ascomatal cavity ± vertically orientated, elongate-clavate to subcylindrical, 80–100 × 10–20 μm, 8-spored. *Ascospores* distichously arranged in the asci, soleiform, 1-septate, constricted at the septum, the lower cell often distinctly smaller and less deeply pigmented, golden brown, verruculose, with a gelatinous sheath to 1·5 μm thick in potassium hydroxide, 19–23(–27) × (7·5–)9–11(–12) μm.

Anamorph: Unknown.

Host: Unidentified bark. Probably lichenized with *Trentepohlia*.

Distribution: India (Andaman Islands).

Observations: This species can be distinguished from the other large-spored species of the genus by both the shape and/or sizes of the ascospores and by the particularly large and erumpent ascomata. The erumpent ascomata recall those of *Peridiothelia*, but in this species are clearly hyphal in structure throughout and the walls incorporate host cells even in their upper parts; the centrum reaction also supports the placement in *Mycomicrothelia*, where it has a rather isolated position.

Two collections of *Verrucaria conothelena* from the Andaman Islands with different collector's numbers are present in H-NYL; that with Nylander's notes is selected here as the lectotype.

The var. *errans*, evidently separated on the basis of a less well developed thallus, is indistinguishable from var. *conothelena* in its microscopic features.

Specimens: **India:** Andaman Islands, 1867, *S. Kurz* 54 (H-NYL 704—lectotype of *Verrucaria conothelena*; M—isolectotype); loc. cit., 1867, *S. Kurz* 55 (H-NYL 706, M); loc. cit., 1867, *S. Kurz* 78 (H-NYL 710—holotype of *V. conothelena* var. *errans*; M—isotype).

8. **Mycomicrothelia dothideaspora** (Cooke & Harkn.) D. Hawksw., **comb. nov.**

Amphisphaeria dothideaspora Cooke & Harkn. in *Grevillea* **14**: 9 (1885).

Fig. 20A–C.

Ascomata arising singly, occasionally confluent at the margins, scattered over the surface of the bark, colonies delimited by a black line, immersed, subepidermal, the epidermis raised to form hemispherical projections; individual ascomata dimidiate, (200–)300–500(–550) μm diam, 120–250 μm tall, black, basal fringe becoming well-marked in older ascomata but rarely exceeding 100 μm wide, fringe distinctly olivaceous green in potassium hydroxide, ostiole slightly depressed; involucrellum dark brown to almost black, somewhat olivaceous green in potassium hydoxide, mainly 20–30 μm thick, consisting of host tissue intermixed with fungal hyphae, hyphae radially orientated, 2–3·5 μm thick, rather uneven in diameter, entering and between the cells of the host, ± smooth-walled, similar to the hyphae in the basal fringe with which it is contiguous; exciple 7–15 μm thick, composed of a variable number of layers of densely interwoven hyphae 2–4 μm thick (textura intricata), compacted, brown to dark brown throughout and continuous below the centrum. *Pseudoparaphyses* cellular, persistent, filiform, numerous, branched and anastomosing, 1·5–3 μm thick. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated, elongate-clavate, short-stalked, bitunicate, with a shallow squared internal apical beak, 80–110 × 14–18 μm, 8-spored. *Ascospores* distichously arranged in the asci, broadly ellipsoid to obovoid, 1-septate, strongly constricted at the septum, cells unequal in size, the lower ⅓–½ the length of the upper and consistently narrower, rounded at the apices, not attenuated, dark olive brown, appearing almost smooth but with a sparse punctate-verruculose ornamentation only seen with difficulty, with a gelatinous sheath *c.* 1 μm thick, 16–19·5 × 7·5–10(–10·5) μm.

Anamorph: Unknown.

Illustrations: Scheinpflug in *Ber. schweiz. bot. Ges.* **68**: 380 fig. 21e (1958).

Exsiccatae: Ellis & Everhart, *N. Am. Fungi* 1662 (sub *Amphisphaeria dothideaspora*;

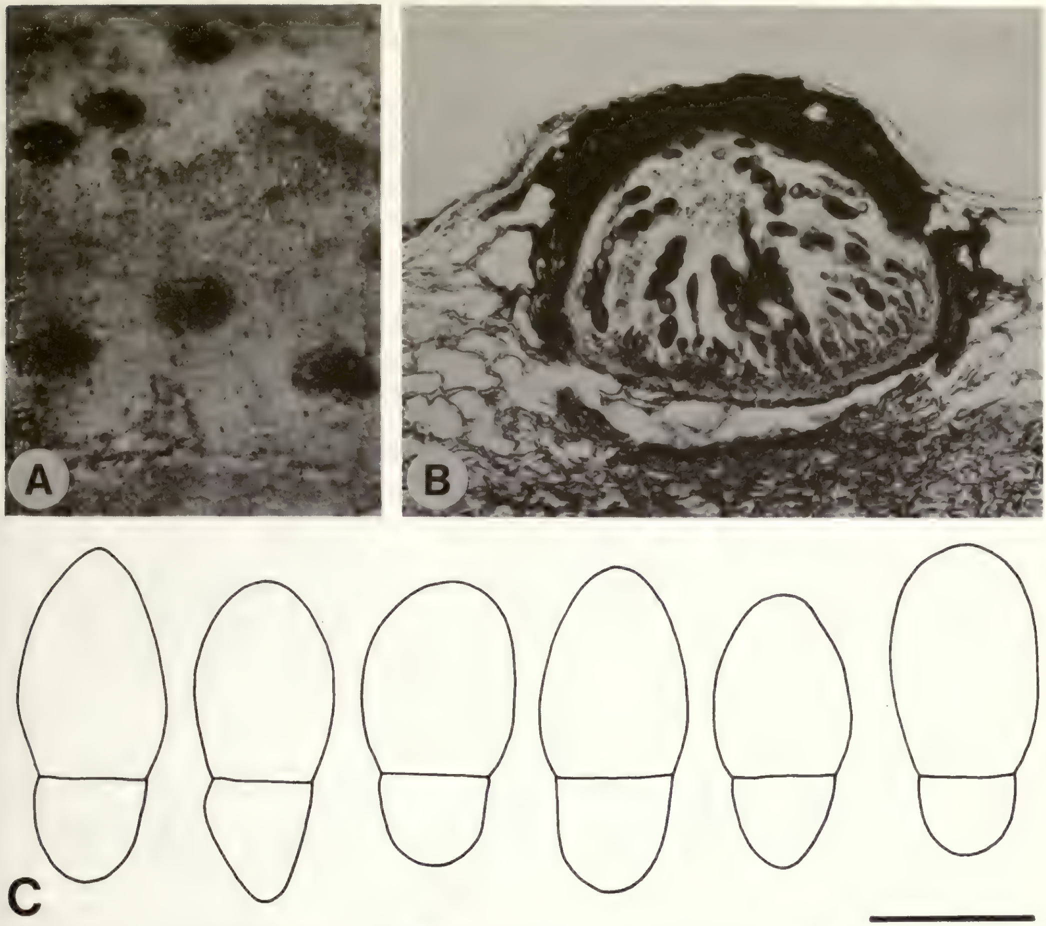

Fig. 20 *Mycomicrothelia dothideaspora* (K—lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

K—isotype of *A. dothideaspora*).—Rabenhorst, *Fungi Eur.* 3553 (sub *A. dothideaspora*; K—isotype of *A. dothideaspora*).

Host: Mimulus glutinosus dead stems.

Distribution: Only known from the extensive original collections of Harkness made in San Francisco, California, U.S.A.

Observations: Scheinpflug (1958: 372) took up the name *Amphisphaeria inaequalis* for this fungus but that species appears to be quite distinct and is treated here as *Mycomicrothelia inaequalis* (p. 90).

In the original description of this species, two collections of Harkness, nos 2217 and 2508, were mentioned; both are present in K. No. 2508, which has annotations probably used in drawing up the description, is designated here as the lectotype.

Scheinpflug indicated that the ascospores could reach 24 × 11 μm, but this may have been due to his inclusion of a second specimen from an unknown host in his concept of the taxon.

The structure of the ascomata in this species is typical of *Mycomicrothelia*, but the species is clearly distinguished by the markedly unequal-celled ascospores as well as the different host. The pseudoparaphyses are very delicate and numerous as is the case in *M. wallrothii*, but have not infrequent septa so are most approximately interpreted as elongated cellular rather than trabeculate pseudoparaphyses.

Additional specimens: **U.S.A.:** California, [San Francisco], on *Mimulus glutinosus, H. W. Harkness* 2508 (K—lectotype of *Amphisphaeria dothideaspora,* isolectotype); loc. cit., *H. W. Harkness* 2217 (K, two specimens).

9. Mycomicrothelia exigua (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia exigua Müll. Arg. in *Bot. Jb.* **6**: 416 (1885).
Verrucaria microthelena [*'micothelena'*] Nyl. in *Flora, Jena* **59**: 364 (1876), nom. inval. (Art. 32.1).
Microthelia intermedia Müll. Arg. in *Bot. Jb.* **6**: 416 (1885).

Figs 21A–C, 22A–B.

Ascomata arising singly, scattered, ascomata emerging through crustose lichens or overgrown by them, perhaps with an independent pale creamy brown thallus delimited by a dark purplish

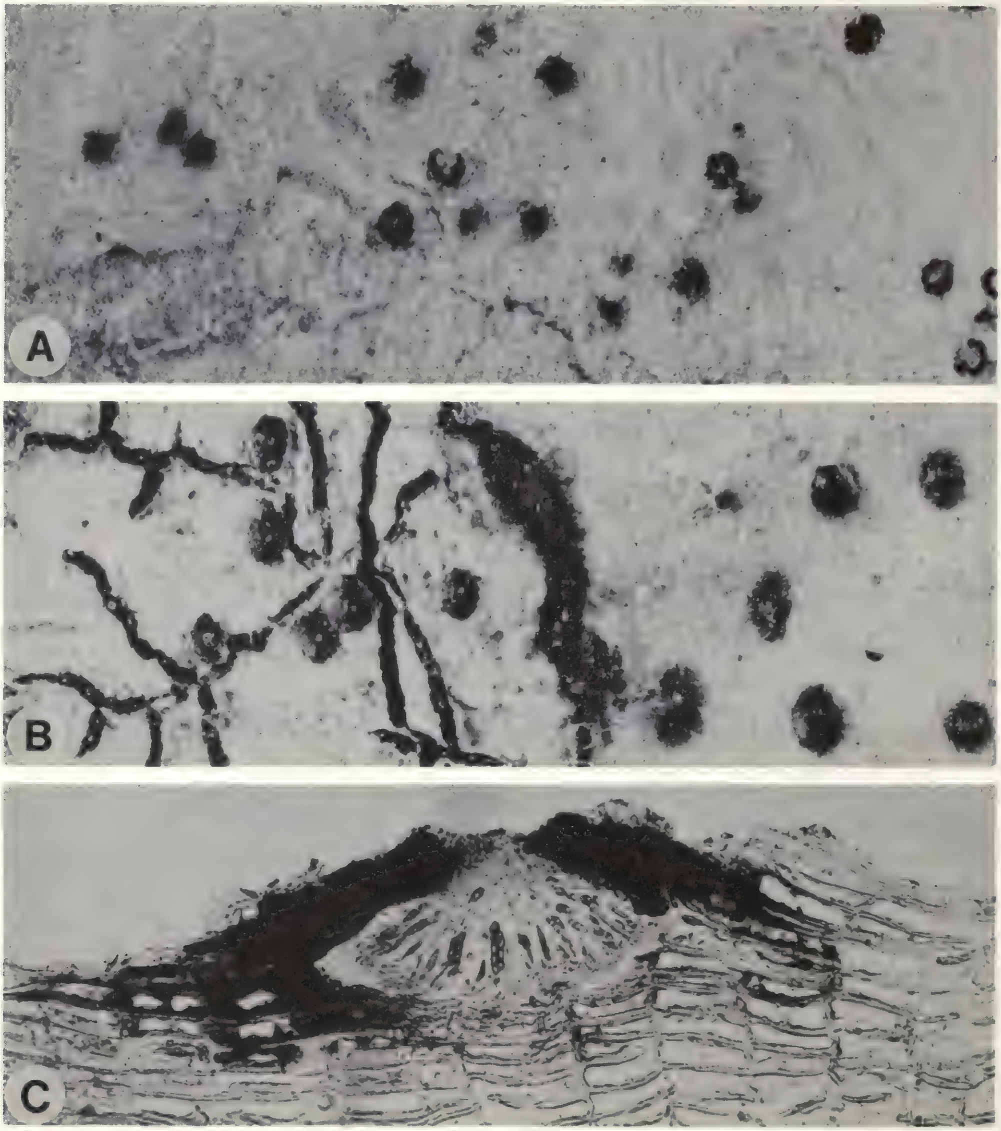

Fig. 21 *Mycomicrothelia exigua.* **A**, Surface view (G—holotype), × 20. **B**, Surface view (G—holotype of *Microthelia intermedia*) showing ascomata erumpent through a graphidean lichen thallus, × 20. **C**, Vertical section of ascoma (G—holotype of *M. intermedia*), × 250.

black line to 0·5 mm wide in places; subperidermal, the surface raised to form low hemispherical projections; individual ascomata dimidiate, applanate, (150–)200–250 μm diam, 80–110 μm tall, black, basal fringe ± absent, ostiole almost plane; involucrellum dark reddish brown, becoming olivaceous in potassium hydroxide, 25–45 μm thick, composed of irregularly arranged hyphae mainly 2–3 μm thick, the cells sometimes becoming occluded, the tissue tending to extend below the generative locule as well as above and marginally, hyphae reddish brown, ± smooth-walled; exciple scarcely differentiated from the involucrellum, composed of 1–2 irregular layers of intertwined hyphae above, hyphae similar to those of the involucrellum; base of the ascomatal cavity not differentiated from the generative tissues; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, filiform, branched only rarely, regularly septate, 1·5–2 μm thick. *Asci* arising from the base and in the angles of the ascomata, orientated towards the ostiole, subcylindrical, short-stalked, bitunicate, with a broad internal apical beak when young, 42–60 × 8·5–12 μm, 8-spored. *Ascospores* distichously arranged in the asci, narrowly ellipsoid to narrowly soleiform, 1-septate, rounded at the apices, not or slightly constricted at the septum, the lower cell slightly smaller, pale olive brown, weakly verruculose, with a thin gelatinous sheath to 1·5 μm thick in potassium hydroxide, 12·5–14(–15·5) × 4–5·5 μm.

Anamorph: Unknown.

Host: Unidentified bark. Perhaps not really lichenized but sometimes erumpent through thalli of other species.

Distribution: Cuba.

Observations: This species is separated from the other small-spored tropical species of the genus, notably *M. fumulosa, M. minutula*, and *M. subfallens*, in the consistently narrower ascospores and asci. The ascospore dimensions recall those of *M. macularis*, but *M. exigua* can be separated from that species on the basis of the much more clearly delimited ascomata, less regularly orientated hyphae of the upper walls, and absence of associated pycnidia.

Müller Argoviensis (1885) appears to have distinguished *Microthelia intermedia* and *M. exigua* primarily on the basis of rather more attenuated basal cells to the ascospores. This character does not, however, hold when a range of spores is examined, and I have no doubt that these collections are conspecific.

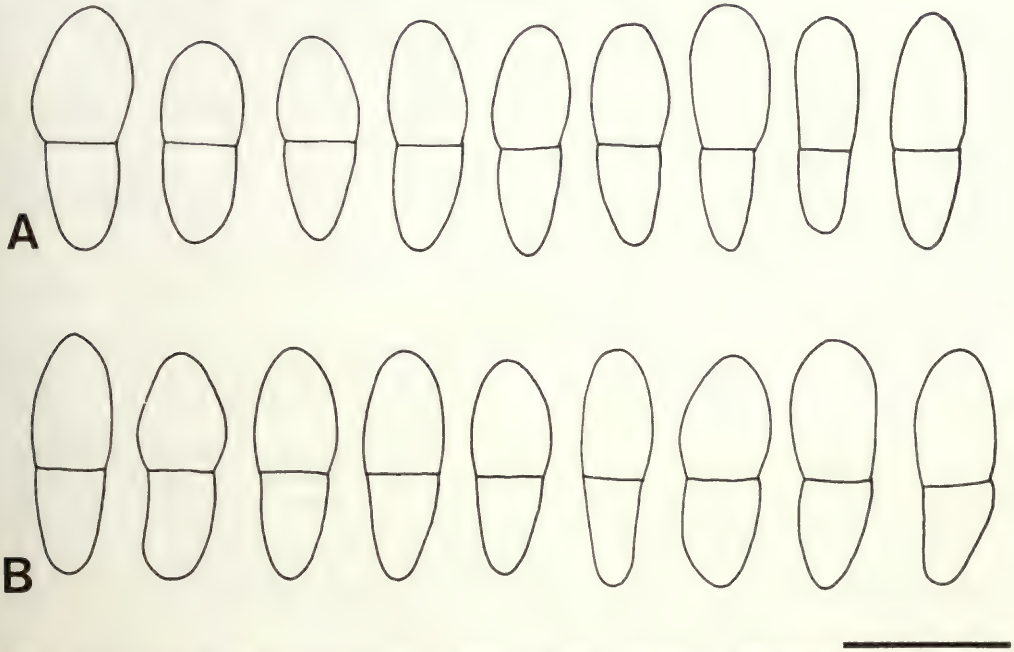

Fig. 22 *Mycomicrothelia exigua* ascospore outlines. **A**, G—holotype. **B**, G—holotype of *Microthelia intermedia*. Scale = 10 μm.

The name *Verrucaria microthelena* was applied by Nylander (loc. cit.) to Wright's *Verruc. Cub*. exs. 14. Müller Argoviensis recognized this, but decided not to take up Nylander's nomen nudum as the resultant combination would have been almost a tautonym.

Specimens: **Cuba:** sine loc., *C. Wright* s.n. (G—holotype of *Microthelia intermedia*); sine loc., *C. Wright* [*Verr. Cub*. exs. 14] (G—holotype of *M. exigua*).

10. Mycomicrothelia fumosula (Zahlbr.) D. Hawksw., **comb. nov.**

Microthelia fumosula Zahlbr. *in* Handel-Mazzetti, *Symbol. sin.* **3**: 18 (1930).

Fig. 23A–F.

Ascomata arising singly, scattered, colonies often delimited by a purplish-black line *c.* 50 μm thick, immersed, subepidermal, the epidermal layers raised to form low hemispherical projections; individual ascomata dimidiate, 175–275(–300) μm diam, 70–110 μm tall, black, with a purplish black basal fringe to 50 μm thick sometimes evident, ostiole depressed or very slightly raised and pushing between the epidermal cells; involucrellum dark reddish brown, slightly olivaceous in potassium hydroxide, mainly 25–40 μm thick, consisting of host cells intermixed with fungal hyphae, hyphae rather irregularly to radiately arranged, 2–3·5 μm thick, very uneven in diameter, mainly in interstices between the host cells, ± smooth-walled; exciple poorly delimited, comprising an irregular number of layers of subhyaline to pale brown interwoven hyphae (textura intricata); the base not delimited from the ascogenous layer or with a few pale brownish hyphae extending into its margins from the adjacent wall layers; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, filiform, sparsely septate, 2–2·5(–3) μm thick, branched and anastomosing. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated or inclined towards the ostiole, elongate-clavate to subcylindrical, short-stalked, bitunicate, no internal apical beak seen, 55–65 × 10–14 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid to soleiform, 1-septate, not to slightly constricted at the septum, the lower cell slightly shorter and narrower, rounded to slightly attenuated at the apices, pale brown to golden brown, slightly verruculose, gelatinous sheath to 1·5–2 μm thick in potassium hydroxide, (11–)12–14(–15) × (5–)5·5–6·5(–7·5) μm.

Anamorph: Minute sporocarps to about 50 μm diam locally abundant on the type collection may represent either pycnidia or young ascomata; no conidia or ascospores were found in the few examined.

Host: Pittosporum floribundum (Pittosporaceae) twigs and unidentified bark. Either not associated with algae or lichenized with *Trentepohlia*.

Distribution: China and Japan.

Observations: This species differs from *Mycomicrothelia minutula* in the consistently smaller spores, and from *M. macularis* in their shape, tending to be more attenuated at the apices.

Zahlbruckner (loc. cit.) recorded asci 85–90 μm long and also indicated that the ascospores were uniseriately arranged in the asci; both these observations may be due to his studying discharging asci.

The specimen from Japan has a rather better developed ascomatal fringe and occurs on almost certainly lichenized pinkish patches on the bark. It may well merit recognition as a separate species but with such limited material I feel that such a decision would be premature.

Specimens: **China:** Prov. Kweischou, 'inter oppida Tuyun et Patschai prope vicum Dodjie', on *Pittosporum glabratum* [i.e. *P. floribundum*], 13 July 1917, *H. F. von Handel-Mazzetti* ('Diar. Nr. 2112') [*Iter sinense* 1914–1918 no. 10.728.] (W 1926/2344—holotype). – **Japan:** Kyushu, Prov. Higo, Ichibu, Kuma-gun, 2 January 1923, *K. Maebara* [hb. Asahina 11767] (TNS).

11. Mycomicrothelia hemisphaerica (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia hemisphaerica Müll. Arg. in *Bot. Jb.* **6**: 417 (1885).

Microthelia intercedens Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **32**: 171 (1894).

Figs 24A–B, 25A–B.

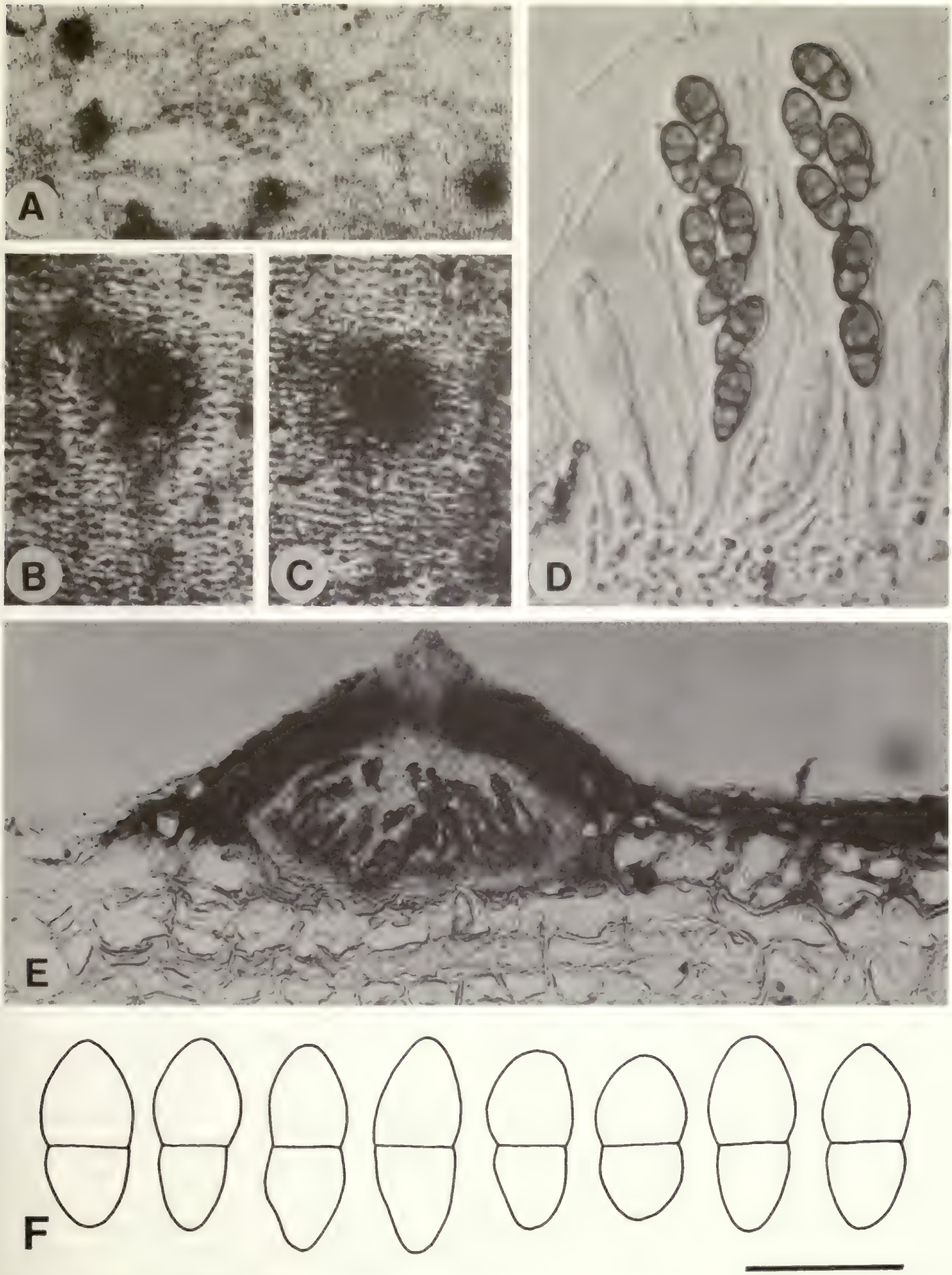

Fig. 23 *Mycomicrothelia fumulosa* (W 1926/2344—holotype). **A**, Surface view of ascomata, × 20. **B–C**, Surface view of ascoma, × 50. **D**, Asci and pseudoparaphyses, × 1020. **E**, Vertical section of ascoma, × 250. **F**, Ascospore outlines, scale = 10 μm.

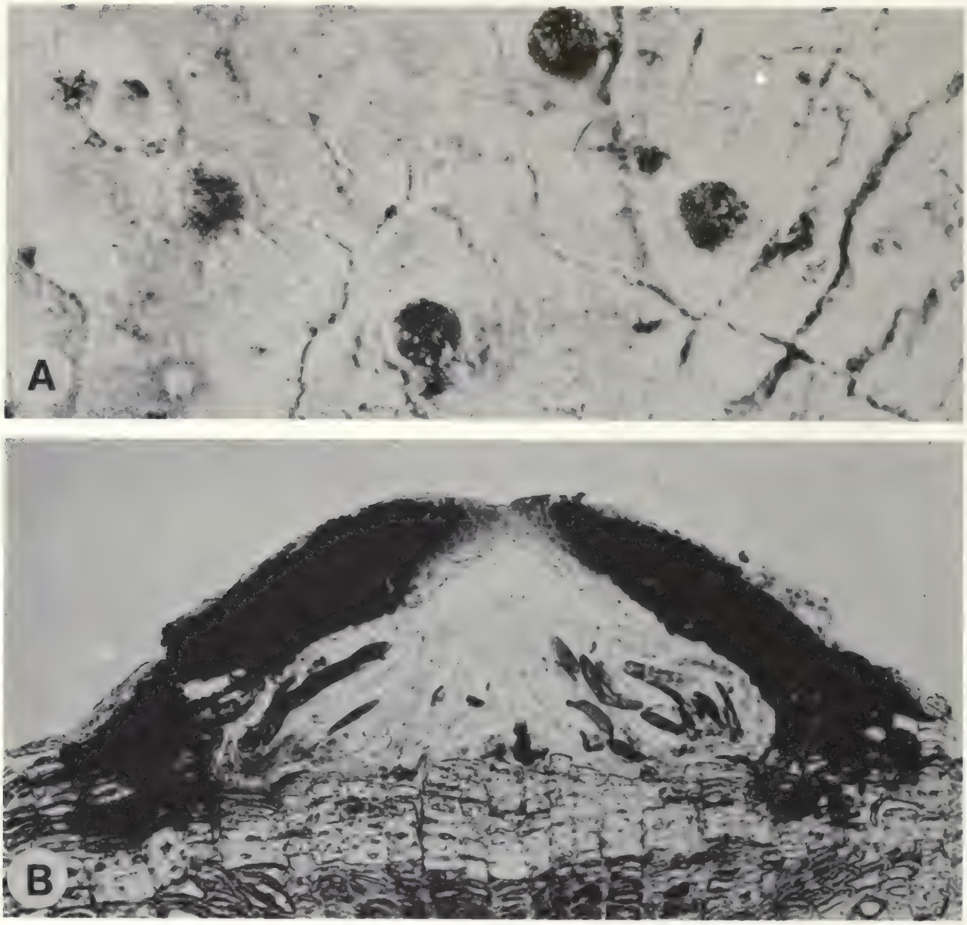

Fig. 24 *Mycomicrothelia hemisphaerica* (G—lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250.

Ascomata arising singly, rather evenly distributed over the whitish thallus, colonies not delimited by a black line, immersed, subepidermal, the outer layers of bark raised to form conspicuous hemispherical projections; individual ascomata dimidiate, applanate at the base, 200–350(–400) µm diam, mainly 150–180 µm tall, basal fringe poorly developed but sometimes extending to about 70 µm, ostiole depressed and visible as a whitish spot 25–40 µm diam, black; involucrellum dark reddish brown, becoming somewhat olivaceous in potassium hydroxide, 35–60 µm thick, consisting of host tissue intermixed with fungal hyphae, hyphae 2–3 µm thick, uneven, smooth-walled, mainly between the host cells at the margins but the host cells eventually becoming almost completely occluded above the centrum; basal tissue of the ascomata scarcely differentiated from the generative tissues or comprising an irregular layer of subhyaline pale brown to subhyaline hyphae, individually 2–3 µm thick; exciple composed of a few layers of interwoven reddish brown hyphae forming a layer reaching about 10 µm thick near the ostiole, forming a textura intricata; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, sparsely septate, filiform, branched and anastomosing, 1·5–2 µm thick. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated to inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a distinct rather clavate internal apical beak when young becoming more cylindrical at maturity, 75–90 × 12–18 µm, 8-spored. *Ascospores* distichously arranged in the asci, elongate-ellipsoid to oblong-ellipsoid, 1-septate, but with 1–2 additional pseudosepta occasionally developing in some spores, only

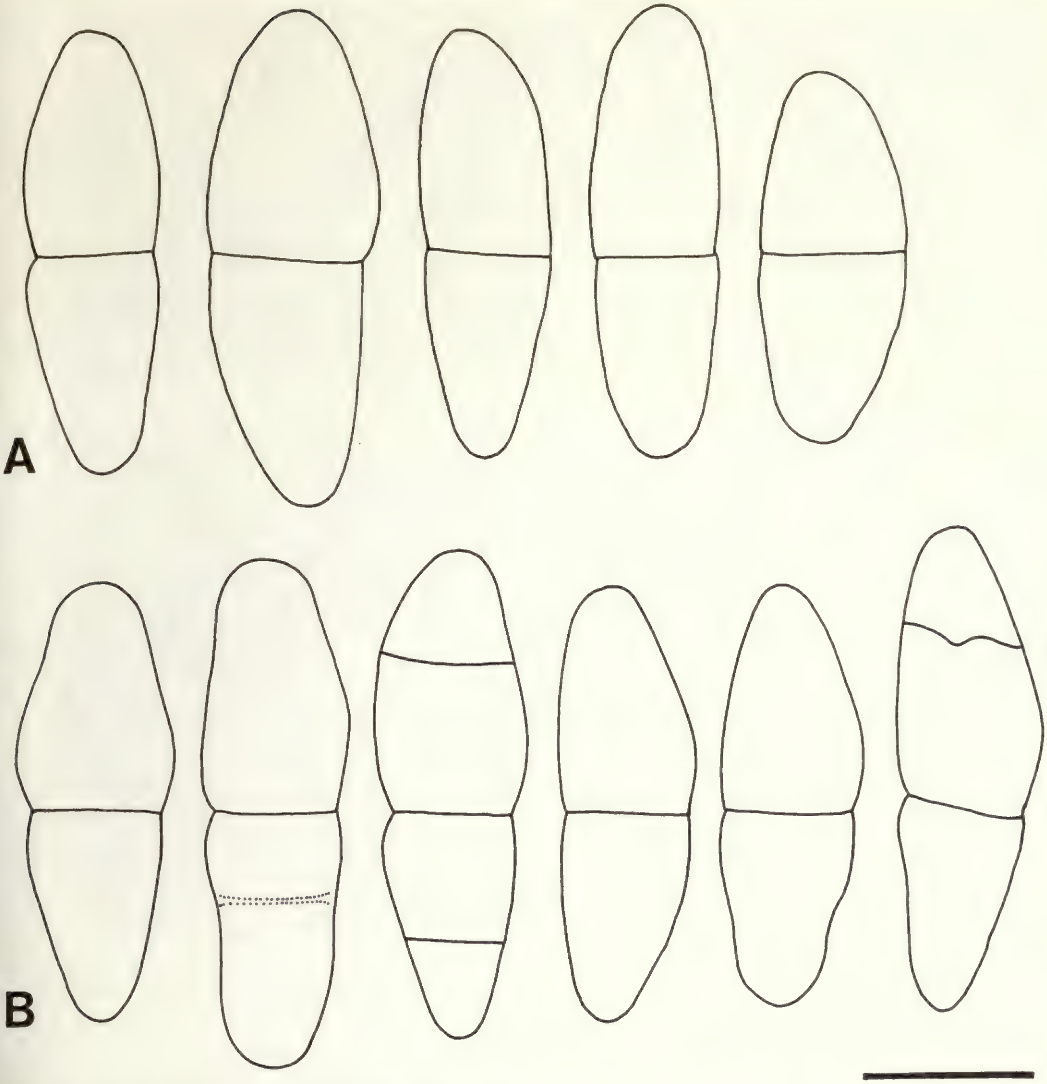

Fig. 25 *Mycomicrothelia hemisphaerica* ascospore outlines. **A**, G—lectotype. **B**, G—lectotype of *Microthelia intercedens*. Scale = 10 μm.

slightly constricted at the septum, cells almost equal in size or the upper slightly larger, apices rounded to rather abruptly truncated, olivaceous brown, rather coarsely verruculose, with a gelatinous sheath 1–2 μm thick in potassium hydroxide, (21–)24–28(–30) × 5–9(–11) μm.

Anamorph: Unknown.

Host: Unidentified bark. Probably lichenized with *Trentepohlia* but algal cells not intimately associated with the ascomata when studied in vertical section.

Distribution: Cuba and Costa Rica. Also mentioned by Müller Argoviensis (1885: 417) from New Caledonia but that material has not been located and may well refer to a different species.

Observations: Two collections were cited in the original account of *Microthelia hemisphaerica*, one from Cuba and the missing specimen from New Caledonia; the former is selected here as the lectotype because it bears detailed notes evidently used in the drawing up of the original description. Two specimens were also cited in the original account of *M. intercedens*, both collected by Pittier in Costa Rica; one was said to be from San José and numbered 6303 and the other from Bourca and numbered 6304. Two collections are present under this name in G, both without numbers; one is labelled as from Bourca (although it has San José also on it and crossed out in Müller's hand) and the other from San José. These belong to different species; that from Bourca is the one described above, while that from San José comes within the range of variation of *Mycomicrothelia captiosa* (p. 73). The lower limit of spore length of 20 μm given in the original description reflects the inclusion of both these disparate elements in Müller's concept of the species. The Bourca specimen is here selected as lectotype as this is the collection with the most detailed annotations and Müller even added 'L. Costar. II. n. 266' after the name citation. The present Art. 69 does not apply as the name has been scarcely used by later workers, and the larger-spored element can be used as a satisfactory type.

Mycomicrothelia hemisphaerica is closely allied to *M. thelena*, which it recalls not only in the whitish thallus but further in the thin pseudoparaphyses, the large ascospores, and tendency of the ascospores to develop additional septa. The two species are, however, clearly separable on the basis of ascospore shape and width.

Specimens: **Costa Rica:** Bourca, Tondaz, 1893, [*H. Pittier* 6304?] (G—lectotype of *Microthelia intercedens*). – **Cuba:** *sine loc., C. Wright* [*Verr. Cub.* exs. 66] (G—lectotype of *M. hemisphaerica*).

12. **Mycomicrothelia inaequalis** (Fabre) D. Hawksw. in *Bot. J. Linn. Soc.* **82**: 55 (1981).

Amphisphaeria inaequalis Fabre in *Ann. Sci. nat.* (Bot.) VI, **9**: 85 (1878).
Kirschsteiniella inaequalis (Fabre) Petrak in *Sydowia* **1**: 213 (1947).
Astrosphaeriella inaequalis (Fabre) Scheinpflug in *Ber. Schweiz bot. Ges.* **68**: 372 (1958).
Microthelia inaequalis (Fabre) E. Müller, *in* Müller & von Arx in *Beitr. KryptogFl. schweiz* **11** (2): 287 (1962).
Kirschsteiniella californica Petrak in *Sydowia* **6**: 353 (1952).

Figs 26A–B, 27A–B.

Ascomata arising singly, scattered, colonies not delimited by a black line, immersed in the outer layers of the wood, the surface raised to form convex but not hemispherical projections; individual ascomata dimidiate, 200–300 μm diam, 150–200 μm tall, basal fringe well-developed, lenticular with the grain of the wood, olivaceous black, extending to 350 μm in the direction of the grain, becoming olivaceous green in potassium hydroxide, ostiole depressed; involucrellum dark reddish brown to almost black, like the hyphal fringe turning olivaceous green in potassium hydroxide, mainly 60–100 μm thick, consisting of host cells intermixed with fungal hyphae, the host cells often remaining distinct, hyphae radially orientated, mainly 3–4 μm thick, rather uneven in diameter, entering and between the host cells, ± smooth-walled and similar to the hyphae in the basal fringe with which it is continuous; exciple 5–10 μm thick, composed of 3–6 layers of densely interwoven hyphae *c.* 2 μm thick (textura intricata), compacted, mainly subhyaline but becoming brownish in the uppermost parts, continuous below the centrum; centrum not reacting with iodine. *Pseudoparaphyses* cellular, persistent, branched and anastomosing, numerous, filiform, frequently septate, 1·5–2·5 μm thick. *Asci* arising from the base of the ascomatal cavity, ± vertically orientated or inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a shallow squared internal apical beak, (65–)70–100 × 15–20 μm, 8-spored. *Ascospores* distichously arranged in the asci, broadly ellipsoid, 1-septate, moderately constricted at the septum, the lower cell consistently somewhat smaller, rounded at the apices, olive-brown to red-brown, apparently smooth-walled, with a thin gelatinous sheath *c.* 1 μm thick, 18–22 × (7·5–)8·5–10·5 μm.

Illustrations: Fabre in *Ann. Sci. nat.* (Bot.) VI, **9**: pl. 2, fig. 15 (1878). – Petrak in *Sydowia* **6**: 356 fig. 1*a* (1952).

Host: Olea europaea, wood. Reports from *Mimulus* are due to confusion with another species (see p. 83) and that from *Buxus sempervirens* (Petrak, 1947) is almost certainly based on a misdetermination.

Distribution: France and the U.S.A. (California).

Observations: Astrosphaeriella inaequalis was wrongly used by Scheinpflug (1958) for

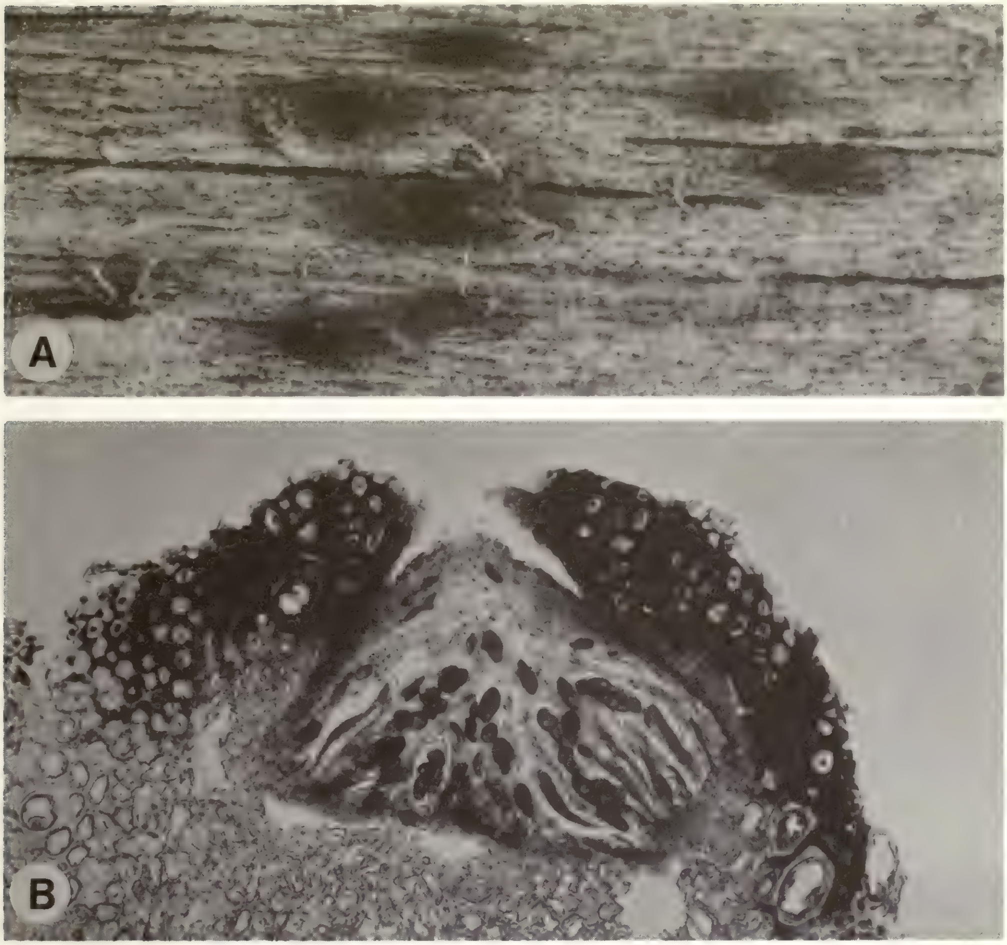

Fig. 26 *Mycomicrothelia inaequalis* (hb Fabre—holotype). **A**, Surface view, × 20. **B**, Vertical section, × 250.

Amphisphaeria dothideaspora Cooke & Harkn., a species which occurs on *Mimulus glutinosus* (see p. 83), which differs in the consistently shorter ascospores and especially in the much smaller lower ascospore cell. The Fabre material at L'Harmas of *Amphisphaeria inaequalis* was not studied by Scheinpflug but, through the courtesy of Dr P. Teocchi, I was able to examine it. This comprises one card with 13 small fragments of bark and wood; several fungi are present, but the extreme left and extreme right-hand pieces both have a fungus agreeing with Fabre's description and drawings and so are considered to be the holotype. Fabre indicated that the ascospores could reach 25 × 12 μm.

The type collection of *Kirschsteiniella californica* now supports very few ascomata but it appears to be inseparable from this species. Its host was not indicated by the collector, but the decorticate twig on the wood of which it grows superficially resembles that of *Olea europea*. This shrub, although not native in California, has been cultivated there for many years.

Amphisphaeria lojkae Rehm, described from *Quercus* wood in Austria, was reported to differ from this taxon in having ascospores 36 × 12 μm; it requires further investigation.

Specimens: **France:** Vaucluse, on *Olea europaea* wood, *H. Fabre* (hb Fabre—holotype of *Amphisphaeria inaequalis*). – **U.S.A.:** California, on indet. twigs, 30 April 1939, *C. L. Shear* (W 1978/02455—holotype of *Kirschsteiniella californica*).

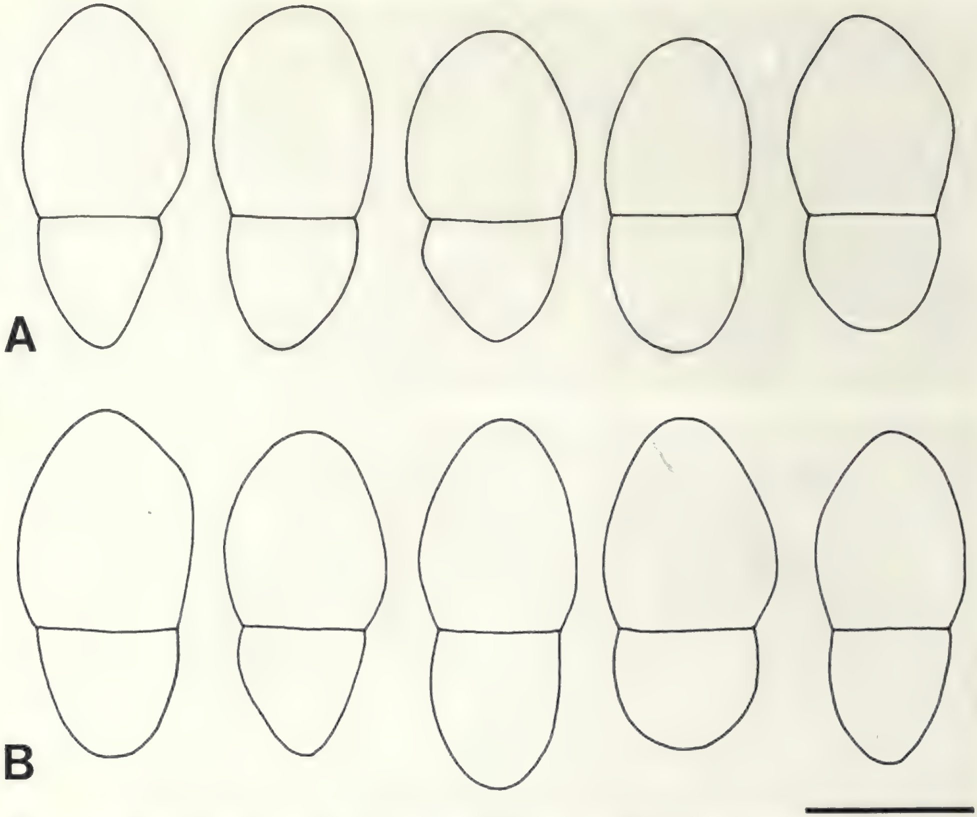

Fig. 27 *Mycomicrothelia inaequalis* ascospore outlines. **A**, hb Fabre—holotype. **B**, W 1978/02455—holotype of *Kirschsteiniella californica*. Scale = 10 μm.

13. Mycomicrothelia macularis (Hampe ex Massal.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 36 (1936).

Microthelia macularis Hampe ex Massal., *Misc. Lich.*: 58 (1856).
Melanospora macularis Hampe *in* Massalongo, *Misc. Lich.*: 58 (1856), nom. inval. (Art. 34.1).
Tomasellia macularis (Hampe ex Massal.) Blomb. & Forss., *Enum. Pl. Scand.*: 105 (1860).
Melanotheca macularis (Hampe ex Massal.) Th. Fr. in *Bot. Notiser* **1866**: 56 (1866).
Microthelia analeptoides Bagl. & Car. in *Comment. Soc. crittogam. Ital.* **1**: 446 (1863).
Verrucaria analeptoides (Bagl. & Car.) Hue in *Revue Bot., Courresan* **6**: 139 (1888), nom. illegit. (Art. 64.1), non *V. analeptoides* Nyl. in *Flora, Jena* **50**: 180 (1867).
Amphisphaeria analeptoides (Bagl. & Car.) Rehm in *Annls mycol.* **4**: 266 (1906).
Didymosphaeria analeptoides (Bagl. & Car.) Rehm *in* Saccardo, *Syll. Fung.* **1**: 715 (1882).
Arnaudiella ribis E. Müller in *Sydowia* **12**: 201 (1959 ['1958']).

Figs 28A–C, 29A–F.

Ascomata arising singly, often abundant, sometimes crowded and then occasionally confluent with adjoining ascomata, bark not discoloured, colonies not delimited, immersed, subepidermal, the epidermis raised to form slightly convex projections, only the ostiole and tissues in its immediate vicinity exposed; individual ascomata dimidiate, 100–175(–200) μm diam, circular to elliptical in surface view, mainly 60–80 μm tall, basal fringe well developed forming a ring to 50 μm wide (consistently narrower on *Ribes*) around the ascomata which is dark brown to black in surface view, ring distinctly olivaceous in potassium hydroxide, ostiole depressed, black; involucrellum dark brown, olivaceous in potassium hydroxide, mainly 9–12 μm thick,

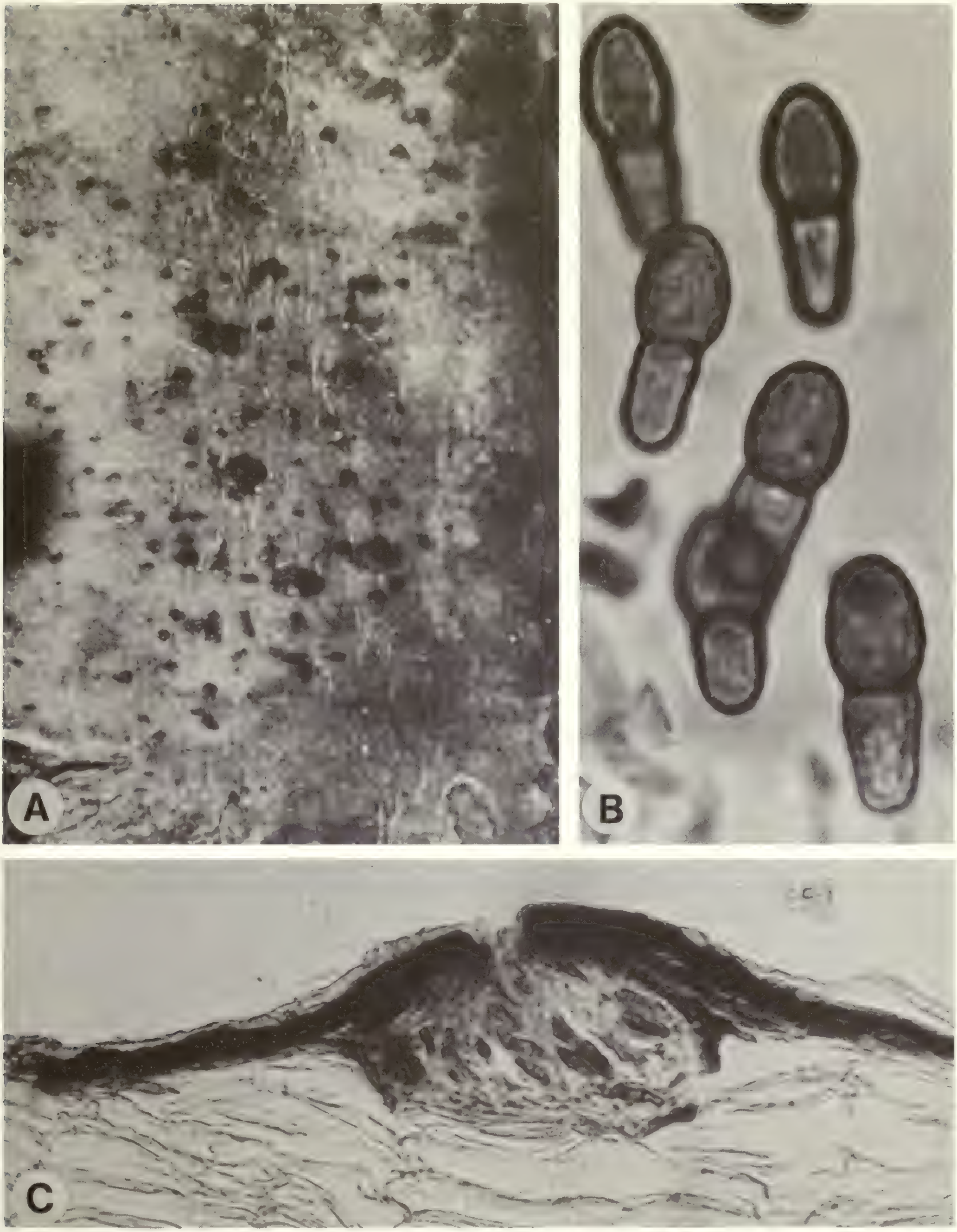

Fig. 28 *Mycomicrothelia macularis*. **A**, Surface view showing ascomata intermixed with pycnidia (*Krypt. Exs. Vindob*. 1354, K), × 20. **B**, Ascospores (ZT—holotype of *Arnaudiella ribis*), × 2500. **C**, Vertical section of ascoma (VER—holotype of *Microthelia macularis*), × 250.

consisting of host tissue intermixed with fungal hyphae, hyphae radially orientated, 2–3 μm thick, rather uneven, irregularly branched, between the host cells, smooth-walled; exciple 2–8 μm thick, composed of 1–5 layers of interwoven hyphae 2–3 μm wide (textura intricata), compacted, ± brown throughout; centrum not reacting with iodine. *Pseudoparaphyses* cellular,

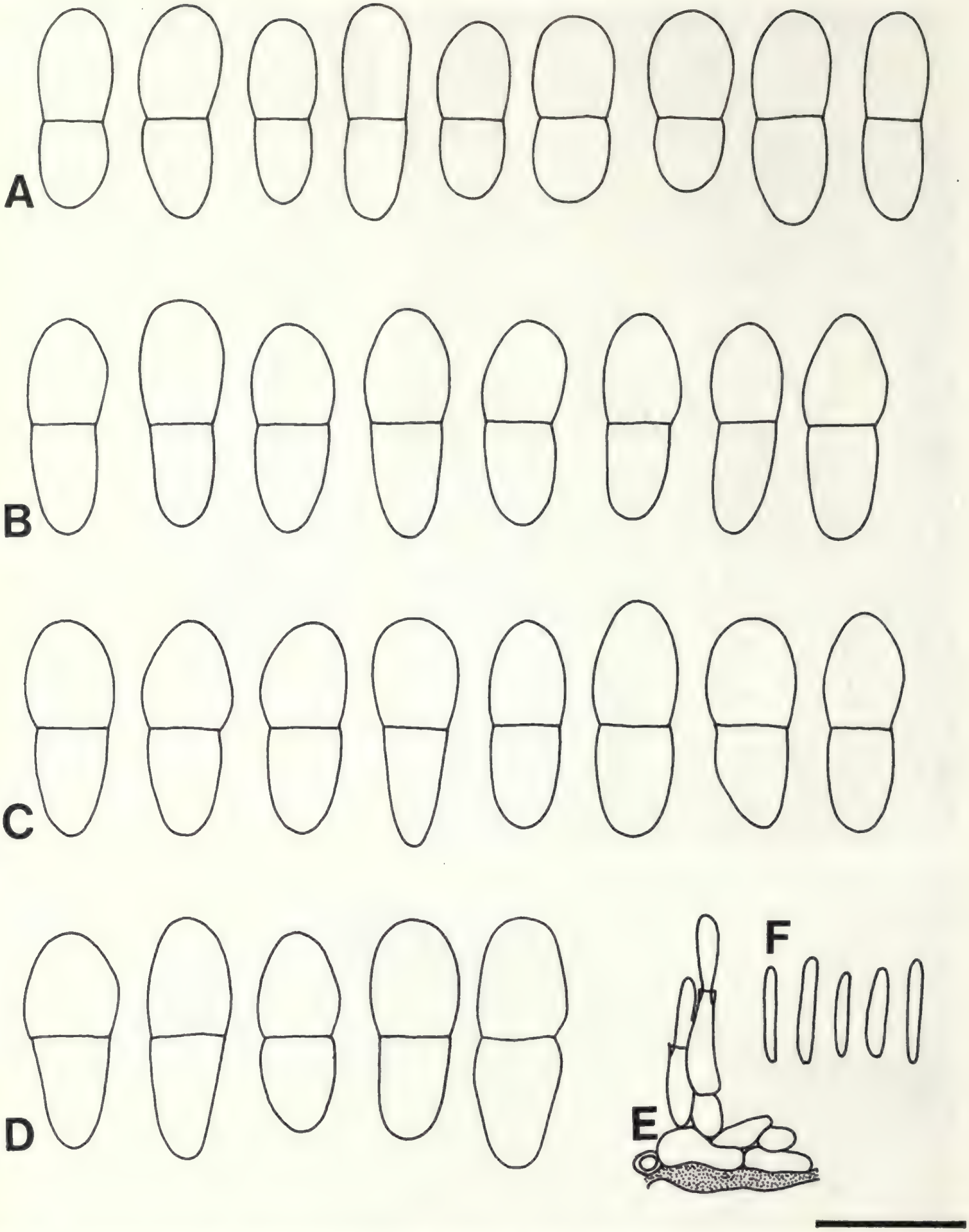

Fig. 29 *Mycomicrothelia macularis* ascospore outlines. **A**, VER—holotype of *Microthelia macularis*. **B**, Arnold, *Lich. Exs.* 423b, K. **C**, ZT—holotype of *Arnaudiella ribis*. **D**, 26 June 1958, *Loeffler*, ZT. **E–F**, Conidiogenous cells and conidia (Lojka, *Lich. Hung.* 116, K). Scale = 10 μm.

persistent, filiform, rather sparse, septate, branched and anastomosing, 2–3 μm thick. *Asci* arising from the tissue lining the base of the ascomata, vertically orientated to inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a rather shallow and broad internal apical indentation, 45–62 × 12–16 μm, 8-spored. *Ascospores* irregularly to distichously arranged in the asci, ellipsoid, 1-septate, constricted at the septum, cells ± equal in size or the upper slightly longer and broader, the ends rounded, not attenuated, golden brown to brown, distinctly verruculose, with a gelatinous sheath swelling to *c.* 2 μm wide in potassium hydroxide, (11·5–)12·5–15(–17·5) × (4–)5–6(–7) μm.

Anamorph: Pycnidia immersed, arising near the ascomata, 30–50 μm diam, black, only the ostiole visible, ostiole *c.* 15 μm diam, deeply pigmented; walls pseudoparenchymatous, cells pale brown, 3–5 μm diam. *Conidiogenous cells* simple, hyaline, elongate-ampulliform, phialidic, 5–8 × 2–3 μm. *Conidia* bacillariform, hyaline, 5–8 × 0·7–1·5 μm.

Hosts: Daphne mezereum, Ribes alpinum, and *R. petraeum* twigs and branches. The host twigs becoming extensively blotched and wrinkled in the case of *Daphne*, but those of *Ribes* are little affected by the presence of the fungus. Evidently not lichenized.

Distribution: Only known from the central European mountains. I have seen material from France, Germany, Hungary, Italy, and Switzerland.

Exsiccatae: Arnold, *Lich. Exs.* 423b (K, sub *Microthelia analeptoides*).—*Erb. Critt. Ital.* 324 (E).—*Krypt. Exs. Vindob.* 1354 (K, sub *M. analeptoides*).—Lojka, *Lich. Hung.* 116 (K, sub *Verrucaria analeptoides*).

Illustrations: Keissler, *Rabenh. Krypt.-fl.* **9**, 1 (2): 25 figs 30–40 (1938).—Müller in *Sydowia* **12**: 202 fig. 1a–c (1959).—Müller & von Arx, *Beitr. Kryptog.-fl. schweiz* **11** (2): 326 fig. 123 p.p. (1962).

Observations: This appears to be a well-defined species unlikely to be confused with any other accepted in the genus here. The spreading basal fringe is a particularly valuable field character, but does occur in a few species on other hosts (e.g. *M. wallrothii*; see p. 115).

Pycnidia are commonly associated with the ascomata but whether they are spermatial or have a role in dispersal is unclear.

Microthelia analeptoides was first described from *Daphne* at Allagna, but the only authentic material I have seen was a packet collected at Riva by Carestia in VER: this is undated but is wrapped in a part of *The Daily Telegraph* dated 30 January 1868 so was probably collected after the species was published in 1863. The VER specimen is consequently designated as a neotype to fix the application of this name. This packet also bears the name '*Microthelia maculiformis* Hampe' in parenthesis, but this epithet does not appear to have been validly published.

Microthelia ribesiella Nyl. ex Vainio was listed as a synonym of *Mycomicrothelia macularis* by Müller & von Arx (1962: 326), presumably without studying the type, as that name proves to be applicable to quite a different taxon (see p. 161). *Arnaudiella ribis* was also placed as a synonym of *M. macularis* by these authors. I have been unable to separate the collections of *Daphne* from those on *Ribes* satisfactorily, and so concur with their view, but it should be noted that the ascospores when on *Ribes* tend to be more commonly over 15 μm long (and exceptionally reach 17·5 μm), and the basal fringe when on this host is less extensive. Such small differences appear to be of little taxonomic importance, but experimental cross-inoculations between the hosts are required to establish the conspecificity unequivocably.

Specimens: **France:** Hautes Alpes, Val Queyras, Aiguilles, on *Ribes petraeum*, 26 June 1958, *W. Loeffler* (ZT). – **Germany:** See Exsiccatae. – **Hungary:** See Exsiccatae. – **Italy:** Riva, on *Daphne mezereum*, *A. Carestia* (VER—neotype of *Microthelia analeptoides*); see also Exsiccatae. – **Switzerland:** [Hercyniae] on *Daphne mezereum*, *E. G. L. Hampe* (VER—holotype of *Microthelia macularis*); Kt. Graubünden, Bergiin, Val Tuors, on *Ribes petraeum*, 26 July 1956, *E. Müller* (ZT—holotype of *Arnaudiella ribis*), *loc. cit.*, 1 July 1959, *E. Müller* (ZT); Kt. Glarus, Braunwald, obere Braunwaldalp, on *R. petraeum*, 18 June 1959, *E. Müller* (ZT); Kt. Wallis, Aletschreservats, Unteraletschwald, on *R. alpinum*, 11 September 1962, *E. Müller* (ZT); Kt. Graubünden, Davos, Dischmatal, Stillberg, on *R. petraeum*, 18 September 1963, *E. Müller & E. Horak* (ZT).

14. **Mycomicrothelia melanospora** (Hepp) D. Hawksw. in *Lichenologist* **14**: 134 (1982).

Pyrenula melanospora Hepp, *Flecht. Eur.* exs. 710 (1860).
Didymosphaeria melanospora (Hepp) Vainio in *Acta Soc. Fauna Fl. fenn.* **49** (2): 151 (1921).
Microthelia koerberi ['Körberi'] Trevisan, *Consp. Verruc.*: 10 (1860), nom. inval. (Art. 32.1).
Verrucaria micula var. *cinereolutescens* Garov., *Tent. Disp. Lich. Langob.*: 79 (1865).

Verrucaria cinerella Flotow ex Zwackh, *Lich. exs.* 37, 217 (1850), nom. inval. (Art. 32.1), nom. illegit. (Art. 64.1).
Microthelia cinerella Flotow ex Zwackh in *Flora, Jena* **45**: 566 (1862).
Pyrenula cinerella (Flotow ex Zwackh) Branth & Rostrup in *Bot. Tidsskr.* **3**: 259 (1869).
Arthopyrenia cinerella (Flotow ex Zwackh) H. Olivier, *Fl. Lich. Orne* **2**: 269 (1884).
?*Epicymatica verrucariaeformis* Fuckel in *Jb. nassau. Ver. Naturk.* **23/24**: 118 (1870).
?*Didymosphaeria verrucariaeformis* (Fuckel) Winter, *Rabenh. Krypt.-Fl.* **1** (2): 429 (1885).
Didymosphaeria epidermidis f. *crataegi* Rehm in *Annls mycol.* **4**: 267 (1906).
Didymosphaeria epidermidis f. *mespili* Rehm in *Annls mycol.* **4**: 267 (1906).

Figs 30A–E, 31A–E.

Ascomata arising singly, scattered, the bark not discoloured in any way, colonies not delimited, immersed, subepidermal, the epidermis raised to form low hemispherical projections, only the ostiole exposed; individual ascomata dimidiate, 150–250(–300) μm diam, mainly 100–125 μm tall, basal fringe forming a ring mainly 30–60 μm wide, black, fringe becoming distinctly olivaceous in potassium hydroxide, ostiole depressed; involucrellum dark brown, becoming distinctly olivaceous in potassium hydroxide, mainly 5–15 μm thick, penetrating between the layers of host cells and the upper epidermal layer becoming separated but also intermixed with host cells especially in the vicinity of the ascomata, hyphae radially orientated when viewed from above, 2–3 μm thick, uneven, ± smooth-walled; exciple mainly 5–10 μm thick but to about 15 μm near the ostiole, composed of 2–5 layers of interwoven hyphae 2–3 μm thick forming a textura intricata, compacted, brown but becoming olivaceous in potassium hydroxide, entire, continuing below the centrum at maturity and pigmented throughout; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, regularly septate, branched and irregularly anastomosed, 2–3 μm thick. *Asci* arising from the tissue lining the base of the ascomatal cavity, ± vertically orientated, broadly clavate, short-stalked, bitunicate, with a small internal apical beak, 42–50 × (15–)18–20(–26) μm, 8-spored. *Ascospores* irregularly distichously arranged in the asci, ellipsoid, 1-septate, scarcely constricted at the septum, cells ± equal in size, rounded at the apices, dark brown, coarsely verruculose, with a thin gelatinous sheath to *c.* 1 μm thick, (12·5–)13·5–15·5(–17) × (6–)6·5–7·5(–8) μm.

Anamorph: Conidiomata intermixed with ascomata, almost always present when the teleomorph occurs but the conidiomata sometimes occur in almost pure stands, scattered, pycnidial, subepidermal, ovoid but vertically compressed, 50–75(–100) μm diam, 50–60 μm tall, black; pycnidial wall developing an involucrellum-like structure above, continuous below the pycnidial cavity, mainly 3–8 μm thick but to 15–18 μm thick near the ostiole, formed of 1–3 layers of compacted interwoven hyphae identical to those of the teleomorph, textura intricata but appearing almost pseudoparenchymatous in parts, brown but distinctly olivaceous in potassium hydroxide. *Conidiogenous cells* arising ± directly from the inner wall of the pycnidium, lacking distinct conidiophores but a few subhyaline pseudoparenchymatous cells often present, enteroblastic, acrogenous, short-ampulliform to short-ellipsoid or almost subcylindrical, phialidic, proliferation not seen, occasionally polyphialidic, hyaline, mainly 5–7 × 4–5 μm. *Conidia* arising singly, not adhering in chains, broadly cylindrical to elongate-ellipsoid, simple and hyaline at first but becoming 1-septate and olivaceous brown to dark brown before release from the pycnidium, not constricted at the septum, rounded at the apex, the base rounded and truncated by a scar 1–1·5 μm wide, smooth-walled, conspicuously 2-guttulate, lacking a gelatinous sheath, 13–14·5 × 5·5–6·5 μm.

Illustrations: Hepp, *Flecht. Eur.* exs. 710 (1860).—Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 15 fig. 19A–B, 26 fig. 41A–C (1936).—Müller & von Arx, *Beitr. Kryptog.-fl. schweiz* **11** (2): 326 fig. 123 (top left) (1962).

Exsiccatae: Arnold, *Lich. Exs.* 147 (sub *Microthelia atomaria*; K).—Hepp, *Flecht. Eur.* 710 (sub *M. melanospora*; G, K).—Körber, *Lich. sel. Germ.* 115 (sub *M. atomaria*; G—lectotype of *Pyrenula melanospora*, M—isolectotype).—Zwackh, *Lich. exs.* 217, 37B (sub *Verrucaria cinerella*; K—37B lectotype of *M. cinerella*).

Host: Mespilus germanicus (syn. *Crataegus germanica*) [Rosaceae], smooth bark. References to occurrences on *Crataegus* s. str. are probably all attributable to nomenclatural confusions as

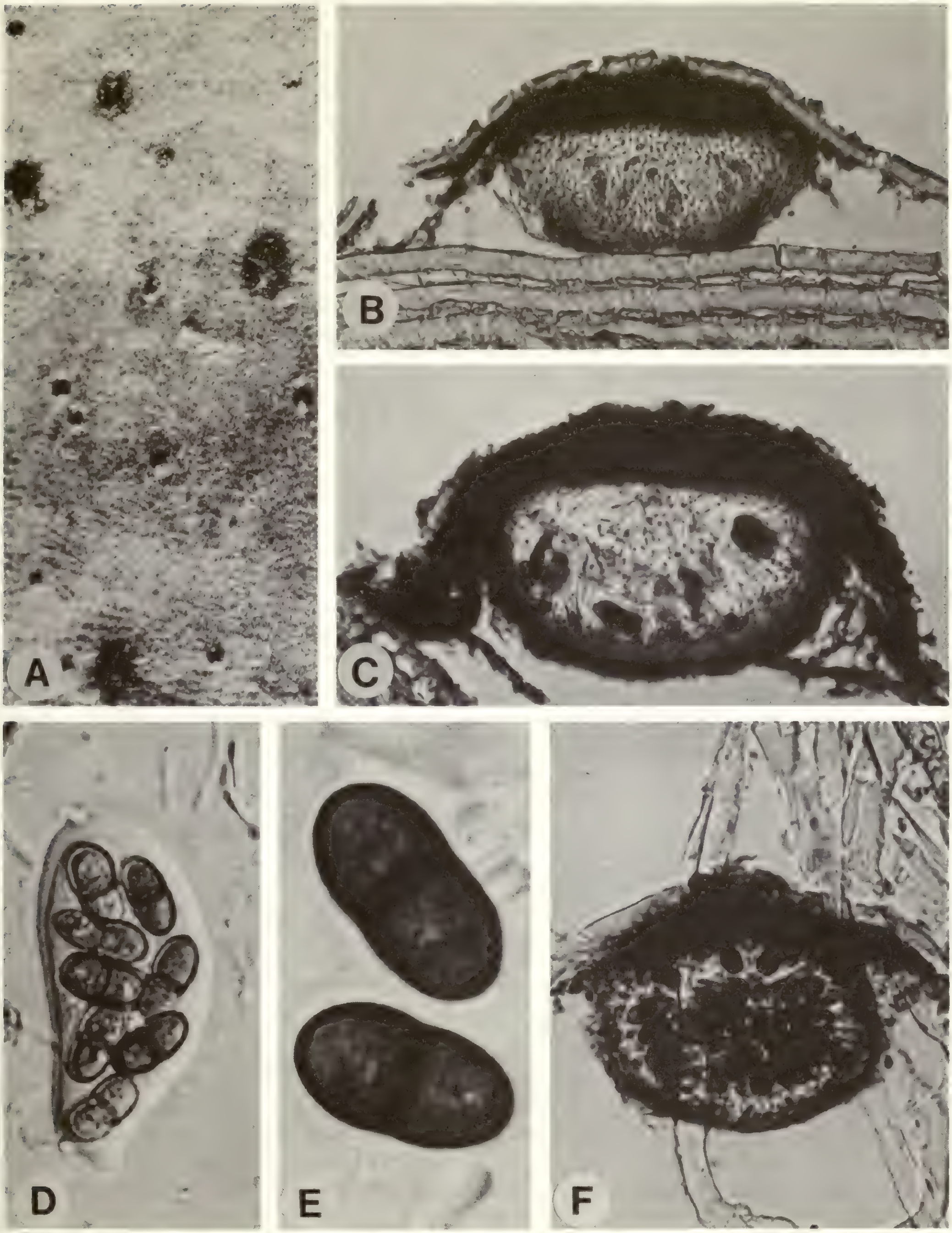

Fig. 30 *Mycomicrothelia melanospora*. **A**, Surface view showing ascomata intermixed with pycnidia (G—lectotype of *Pyrenula melanospora*), × 20. **B**, Vertical section of young ascoma (K—lectotype of *Verrucaria cinerella*), × 320. **C**, Vertical section of mature ascoma (material as **B**), × 320. **D**, Ascus (material as **A**), × 1020. **E**, Ascospores (material as **A**), × 2500. **F**, Vertical section of pycnidium (material as **B**), × 320.

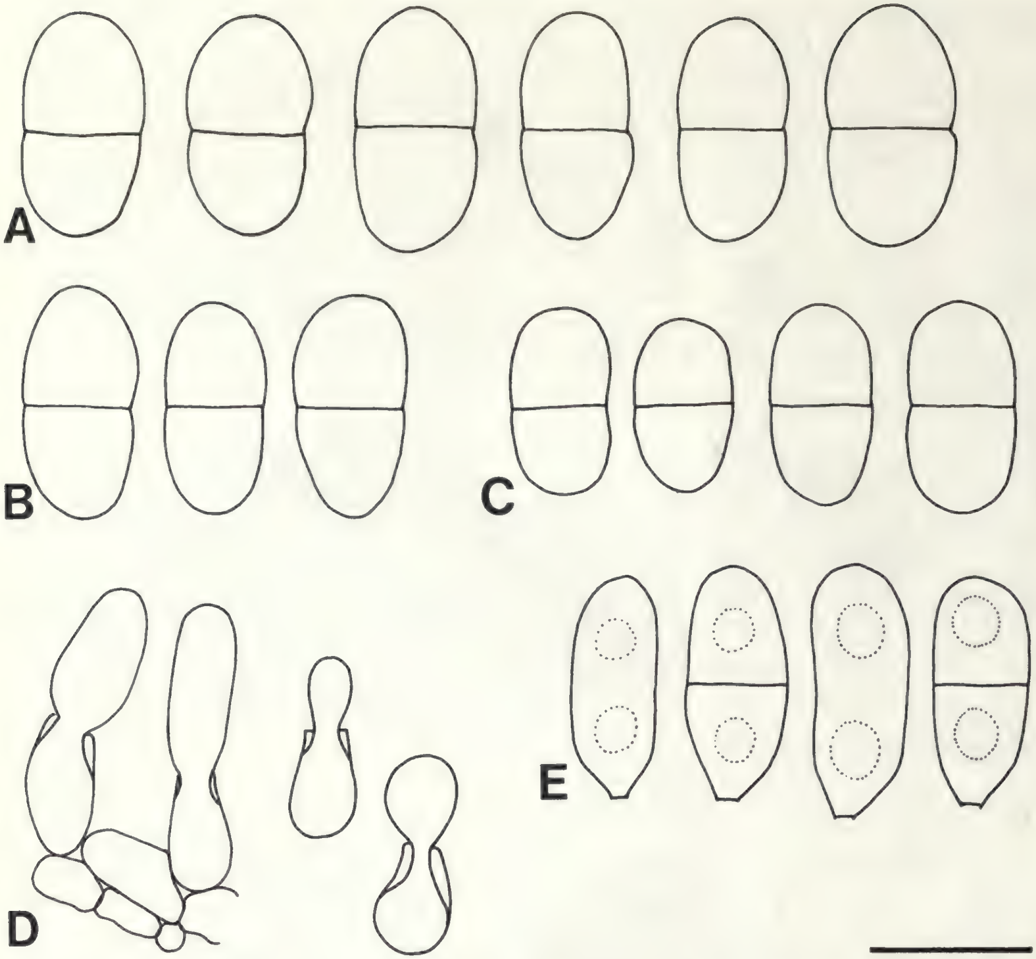

Fig. 31 *Mycomicrothelia melanospora.* **A–C**, Ascospore outlines; **A**, G—lectotype of *Pyrenula melanospora*; **B**, Zwackh, *Lich. Exs.* 217, K; **C**, Arnold, *Lich. Exs.* 147, K. **D**, Conidiogenous cells (material as **A**). **E**, Conidia (material as **A**). Scale = 10 μm.

to the generic position of *M. germanicus*. Keissler (1936: 33) mentions an occurrence on *Sorbus* in Norway, but this is probably due to confusion with *Mycomicrothelia confusa* which can grow on that host and has been seen on it by me from Norway (see p. 80). Not lichenized.

Distribution: Probably widespread in central Europe where the host occurs. I have seen material from Germany, Poland, and Switzerland; there are published reports at least from France (Ozenda & Clauzade, 1970), Italy (Jatta, 1911), and the U.S.S.R. (Kopaczevskaja et al., 1977). References to its occurrence in the British Isles and Norway are probably errors based on confusion with *M. confusa*.

Observations: The epithet *'atomaria'* has been repeatedly applied to this species since the 1850s but cannot be used for any *Mycomicrothelia* (see p. 135). The nomenclature of the epithet *'cinerella'* is complex as it has been used in a variety of senses; the reasons for its placement here are discussed below (p. 142).

The material distributed under the name *Pyrenula melanospora* in Hepp's exsiccatum, cited above, includes the anamorph which predominates in the sets seen. However, the name should not be applied merely to the anamorph because after the citation of the new epithet Hepp cites as synonyms '*Microthelia atomaria* Körb. Syst. p. 373 et Lich. sel. germ. No. 115! *Verrucaria* *punctiformis, atomaria, stigmatella, cinerea* et *punctata* Auct. pr. p.', and it is quite clear that he was introducing a name inclusive of the teleomorph to replace *atomaria* sensu Körber, non Ach. Körber's exsiccatum is also therefore a syntype and was studied by Hepp; I have selected it as the lectotype for Hepp's name, as the teleomorph is abundant on it. Trevisan (1860) simultaneously realised that Körber had misapplied Acharius' epithet, but in introducing *M. koerberi* only stated '*M. atomaria Körb.* exs. 115' and gave no description; as Körber also failed to provide a diagnosis on his exsiccatum label, Trevisan's name is not validly published (Art. 32.1).

I have not seen any type or authentic material of *Verrucaria micula* var. *cinereolutescens* Garov. This was based on a collection from '*Crataegus*' originally determined as *atomaria*; it can consequently be expected to belong here, although the spore measurements were originally given as 12.8–14·2 × 4·2 μm.

Epicymatica verrucariaeformis Fuckel is listed as a possible synonym since it was described from *Crataegus* in Jura, and is reported to have ascospores 14–17 × 6 μm (Keissler, 1930: 480); I have seen no type or authentic material.

Rehm's forms cited above were based on Zwackh's exsiccatum 217a and Hepp's 710; the names are perhaps not validly published (Art. 32.1) but the host restriction itself might be interpreted as diagnostic in the view of the describing author.

Mycomicrothelia melanospora is a distinctive fungus coming closest to *M. confusa*, which differs in the shape of the spores and their length, *M. macularis*, which has narrower and more unequally celled ascospores, and *M. wallrothii*, distinguished by the much more conspicuous basal fringe and further by the anamorph of that species only having simple conidia.

The occurrence of an anamorph in this species does not appear to have been appreciated in recent years, although Hepp (loc. cit.) figured some conidia.

Specimens: **Germany:** 'An *Crataegus* bei Insbach', 1860, *Käyser* [Arnold, *Lich. Exs.* 147] (K). – **Poland:** 'Cavalierberg prope Hirschbergam Silesiae', 'ad *Crategus*', *G. W. Körber* [*Lich. Sel. germ.* 115] (G—lectotype of *Pyrenula melanospora*; K, M—isolectotypes); 'Hirschberg/Silesia', *J. Flotow* (Zwackh, *Lich. Exs.* 37, 217] (K). – **Switzerland:** Zurich, 'auf den rinde von *Mespilus germanicus*', *P. Hepp* [*Flecht. Eur.* 710] (K).

15. **Mycomicrothelia miculiformis** (Nyl. ex Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia miculiformis Nyl. ex Müll. Arg. in *Bot. Jb.* **6**: 417 (1885).
Verrucaria miculiformis Nyl. in *Flora, Jena* **59**: 364 (1876), nom. inval. (Art. 32.1).
Verrucaria miculiformis var. *detincta* Nyl. in *Flora, Jena* **59**: 364 (1876), nom. inval. (Art. 32.1).
Microthelia miculiformis var. *detincta* Nyl. ex Müll. Arg. in *Bot. Jb.* **6**: 417 (1885).
Didymosphaeria detincta (Nyl. ex Müll. Arg.) Vainio in *Ann. Acad. Sci. fenn.* A, **6** (7): 211 (1915).
Verrucaria miculiformis var. *distincta* Hue in *Nouv. Archs. Mus. Paris*, III, **4**: 126 (1892), as 'Nyl.', nom. inval. (Art. 34.1).

Fig. 32A–D.

Ascomata arising singly, exceptionally 2–3 confluent at the base, scattered, colonies whitish to pale brown, delimited by a black line 50–100 μm thick, subperidermal, the surface raised to form low hemispherical projections; individual ascomata dimidiate, (200–)250–350(–400) μm diam, (80–)100–140 μm tall, black, basal fringe generally indistinct from above but extending to about 75 μm around the ascomata in places, ostiole slightly depressed and 25–50 μm wide; involucrellum pseudostromatic, dark reddish brown, becoming olivaceous brown in potassium hydroxide, mainly 35–45 μm thick, consisting of host cells intermixed with fungal hyphae, the hyphae irregularly orientated, 2·5–3·5 μm thick, very uneven in diameter, richly branched, reddish brown, in the interstices of the host cells and also sometimes entering them with the host cells finally becoming occluded, especially in the upper parts; exciple poorly differentiated, mainly consisting of a few interwoven reddish brown hyphae forming a layer only 3–6 μm thick, but to about 15 μm thick close to the ostiole; basal tissue not differentiated from the generative locule; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, filiform, rather sparsely branched, regularly septate, 1·5–2·5(–3) μm thick. *Asci* arising from the base of the ascomatal cavity and also in the angles of the ascomata, orientated towards the ostiole,

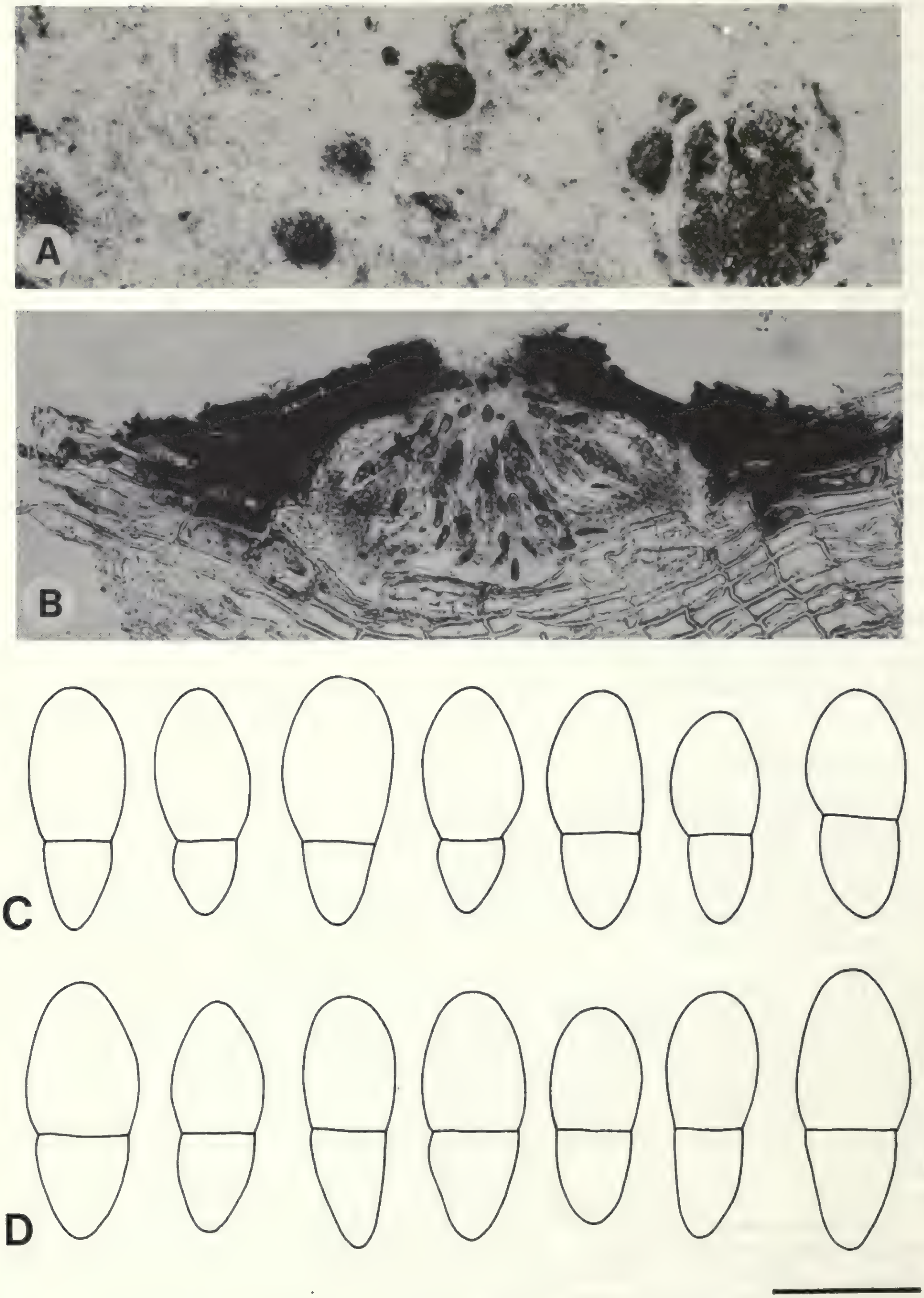

Fig. 32 *Mycomicrothelia miculiformis*. **A**, Surface view (G—holotype of *Microthelia miculiformis*), × 20. **B**, Vertical section of ascoma (material as **A**), × 250. **C–D**, Ascospore outlines (**C** material as **A**; **D** BM—isotype of *M. miculiformis* var. *detincta*), scale = 10 μm.

elongate-clavate to subcylindrical, short-stalked, with a small squared internal apical beak when young, bitunicate, 65–80 × 12–15 μm when mature, 8-spored. *Ascospores* distichously to almost overlapping monostichously arranged, soleiform, 1-septate, constricted at the septum, the lower cell consistently smaller and often also rather paler in colour, rounded to slightly attenuated at the apices, brown, weakly verruculose, gelatinous sheath to 1·5 μm thick in potassium hydroxide, 14·5–17·5(–19) × 6–7·5 μm.

Anamorph: Unknown.

Host: Unidentified smooth bark. The species is almost certainly lichenized with endophloeodal *Trentepohlia*.

Distribution: Cuba. Known only from the rich material of the original collection.

Observations: This species is closest to *Mycomicrothelia captiosa*, but differs in the much shorter ascomata, and perhaps also in the somewhat shorter ascospores. I considered uniting these two species, but as the ascomatal height appears to be consistently less in this species, they are retained as separate until further collections become available. Müller Argoviensis (1885) distinguished *detincta* by the less developed thallus which was concentrated around the ascomata, but this feature is presumably environmentally influenced and scarcely merits taxonomic recognition; Hue's (loc. cit.) usage of '*distincta* Nyl.' was presumably a *lapsus* for '*detincta*'. *M. fumulosa* has distinctly shorter ascospores, *M. exigua* narrower and shorter ascospores which are also more constricted at the septum and smaller ascomata, and *M. subfallens* both smaller ascomata and consistently rather shorter ascospores.

Specimens: **Cuba:** *sine loc., C. Wright* [*Verr. Cub.* exs. 68] (G—holotype of *Microthelia miculiformis*; BM, G—isotypes); *sine loc., C. Wright* [*Verr. Cub.* exs. 87] (BM—isotype of *M. miculiformis* var. *detincta*).

16. Mycomicrothelia minutissima (Knight) D. Hawksw., *in* Galloway in *N.Z. Jl Bot.* **21**: 195 (1983).

Verrucaria minutissima Knight in *Trans. Proc. N.Z. Inst.* **8**: 324 (1876).
Microthelia minutissima (Knight) Zahlbr., *Cat. Lich. Univ.* **1**: 264 (1921).
Microthelia knightiana Müll. Arg. in *Bull. Soc. r. bot. Belg.* **31**: 41 (1892), nom. illegit. (Art. 63.1).

Fig. 33A–C.

Ascomata arising singly but commonly 2–3 confluent, scattered, on a brownish endophloeodal thallus, colony margins not represented in the material studied, immersed, the upper layers of the bark raised to form low hemispherical projections; individual ascomata dimidiate, 200–350 μm diam, to 150 μm tall, black, basal fringe usually poorly delineated but extending to about 125 μm in some fruits; ostiole depressed, the centrum visible as a white spot, gaping, 40–50 μm diam; involucrellum dark reddish-brown, ± unchanged in potassium hydroxide, 20–30 μm thick, consisting of host cells intermixed with fungal hyphae, hyphae irregularly orientated, 2–3 μm thick, very uneven in diameter, richly and irregularly branched, surrounding and entering the host cells which can become occluded, smooth-walled; exciple to 10 μm thick, composed of interwoven almost hyaline hyphae (textura intricata), the base similar but poorly differentiated from the generative tissues; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, abundant, persistent, filiform, branched and anastomosing, septate, 1·5–2 μm thick. *Asci* arising from the base of the ascomatal cavity, orientated towards the ostiole, elongate-clavate to subcylindrical, short-stalked, bitunicate, with a distinct internal apical beak when young, but the beak less well marked when mature, 65–75 × 12–14 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid to soleiform, 1-septate, slightly constricted at the septum, the lower cell somewhat shorter and narrower, the apex rounded and the base rounded to slightly attenuated, pale olivaceous brown, verruculose, without a distinct gelatinous sheath (in potassium hydroxide), 17–22(–24) × 5·5–7·5 μm.

Anamorph: (?) intermixed with the ascomata. *Conidiomata* pycnidial arising singly to ± confluent, similar in structure to the ascomata, black, 75–100 μm wide. *Conidiogenous cells* enteroblastic, acrogenous, elongate-ampulliform, phialidic, sometimes proliferating, hyaline, 5–8 × 2–2·5 μm. *Conidia* arising singly, bacillariform, simple, hyaline, 4–5 × 1–1·5 μm.

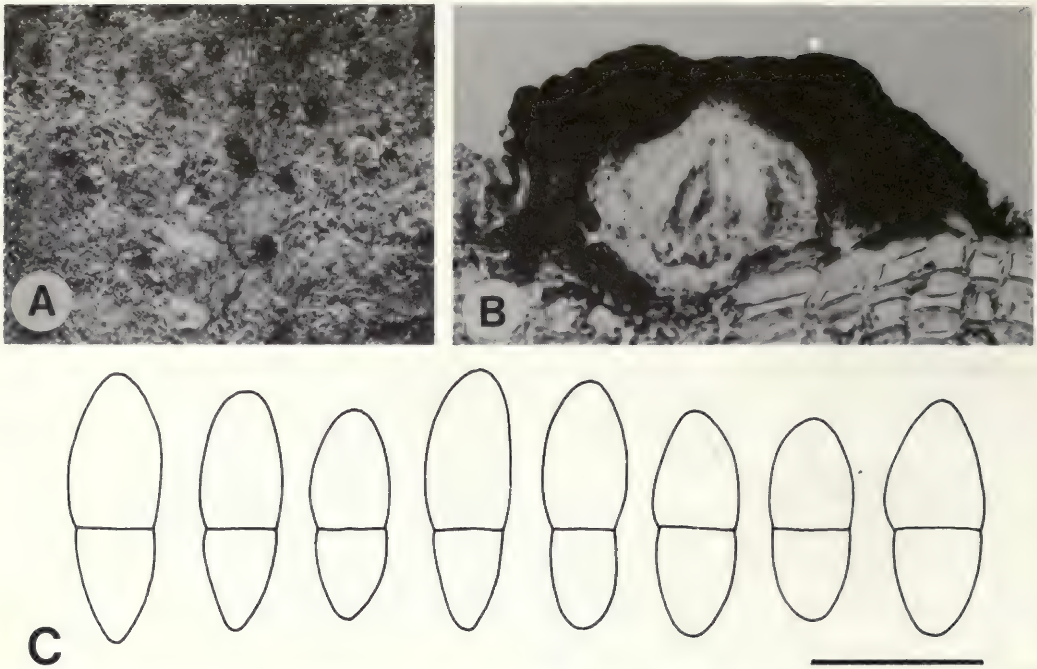

Fig. 33 *Mycomicrothelia minutissima.* **A**, Surface view (BM—isotype), × 20. **B**, Vertical section of ascoma (material as **A**), × 400. **C**, Ascospore outlines (WELT—holotype), scale = 10 μm.

Illustrations: Knight in *Trans. Proc. N.Z. Inst.* **8**: pl. 10 fig. 20, 2a (1876); *Trans. Linn. Soc. Lond.* II, **1**: tab. 37 fig. 21 (1877).

Host: On unidentified bark. Possibly lichenized with *Trentepohlia* but biological status uncertain.

Distribution: New Zealand. Only known from the original collection.

Observations: The presumed anamorph predominates in the holotype and the two probable isotypes in BM and two further isotypes in M. Ascomata were best developed in the holotype in WELT, and in one of the BM collections only hyaline ascospores were seen. On the basis of the latter, and before I had located the holotype, I was therefore inclined to refer this species to *Arthopyrenia* Massal. s. str. In the holotype the ascospores turn brownish while still within the asci so the taxon is appropriately placed in *Mycomicrothelia*.

This species most strongly recalls the North American *M. willeyana*, which also has similar pycnidia, but differs from that species in the narrower ascospores and slightly longer conidia. *M. socialis* has much more regularly aggregated ascomata and much shorter conidia. *M. minutissima* is separated from *M. captiosa* by the less swollen and longer ascospores and the presence of pycnidia.

As the name *Microthelia knightiana* is illegitimate under Art. 63.1 it must be typified by the type of Knight's earlier epithet (Art. 7.11).

Specimens: **New Zealand:** [near Wellington], *C. Knight* (WELT—holotype of *Verrucaria minutissima*; BM, M—isotypes).

17. **Mycomicrothelia minutula** (Zahlbr.) D. Hawksw., **comb. nov.**

Microthelia minutula Zahlbr., *in* Handel-Mazzetti, *Symbol. sin.* **3**: 18 (1930).

Fig. 34A–C.

Ascomata arising singly, scattered, colonies apparently delimited by a black line but this perhaps due to adjacent thalli of lichens, immersed, subepidermal, the epidermis raised to form low

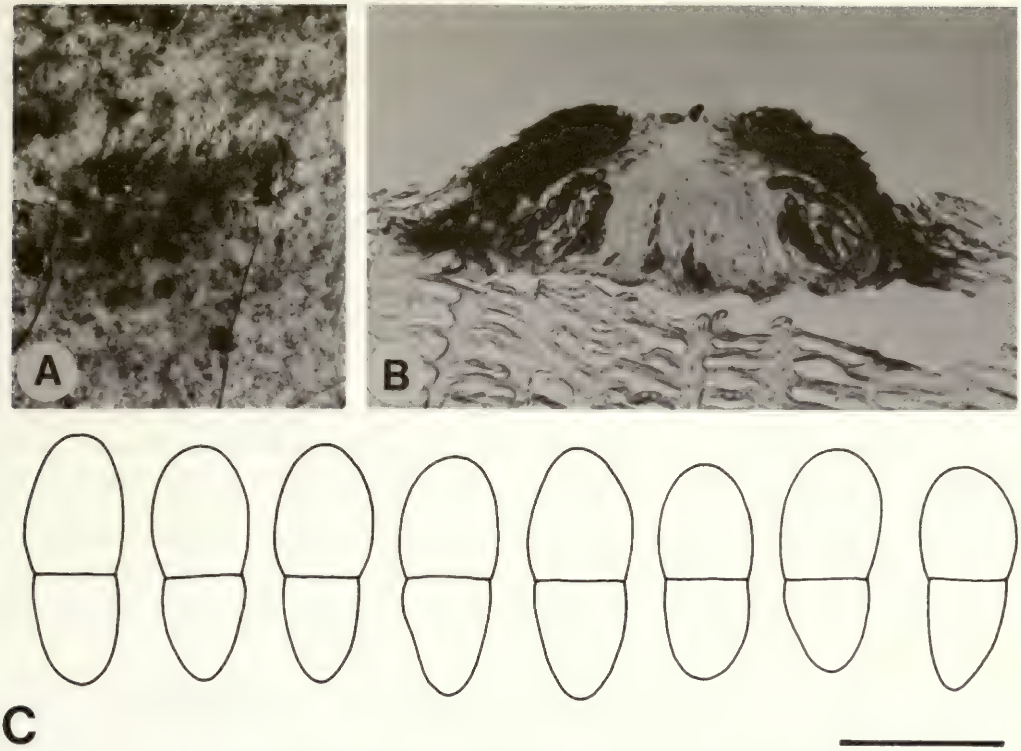

Fig. 34 *Mycomicrothelia minutula* (W 1928/6071—lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

hemispherical projections; individual ascomata dimidiate, (125–)160–200(–275) μm diam, 60–110 μm tall, black, basal fringe poorly developed, scarcely extending beyond the limits of the generative locule, ostiole somewhat depressed; involucrellum dark reddish brown, scarcely changed in potassium hydroxide, 14–35 μm thick, consisting of host cells intermixed with fungal hyphae, hyphae rather irregularly orientated, 2·5–3·5 μm thick, uneven in diameter, entering the cells of the host which often become occluded, smooth-walled; exciple 5–10 μm thick, composed of interwoven hyphae similar to those in the involucrellum but rather paler brown (textura intricata); base composed of subhyaline to pale brown interwoven short-celled hyphae, scarcely delimited from the ascogenous layer; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, branched and anastomosing, numerous, filiform, frequently septate, mainly 1–1·5 μm thick. *Asci* arising from the base of the ascomatal cavity, vertically orientated in the centre but otherwise inclined towards the ostiole, elongate-clavate to subcylindrical, short-stalked, bitunicate, with a squared internal apical beak, 55–65 × 12–14 μm, 8-spored. *Ascospores* distichously to irregularly arranged in the asci, ellipsoid to almost soleiform, 1-septate, slightly constricted at the septum, the lower cell usually slightly shorter and narrower, rounded at the apices or with the lower somewhat attenuated, olive brown, indistinctly verruculose, gelatinous sheath *c.* 1 μm thick (hardly swelling in potassium hydroxide), (12·5–)13·5–15(–16) × (5·5–)6–6·5(–7) μm.

Anamorph: Unknown.

Hosts: Schoepfia jasminodora [Oleaceae] and (according to the original description) *Schizophragma integrifolium* [Saxifragaceae] bark. Apparently not lichenized.

Distribution: China.

Observations: This species is close to *Mycomicrothelia subfallens* but differs in the almost complete absence of a basal fringe, and the more erumpent ascomata (see p. 111).

Two collections were cited in the original account, both from Handel-Mazzetti's expedition to China, but only one was available from W; this is designated here as the lectotype.

Specimen: **China:** Prov. Yunnan, 'prope vicum Tjintjischan ditionis oppidi Loping', on *Schoepfia jasminodora*, 12 June 1917, *H. F. von Handel-Mazzetti* ('Diar. Nr. 1976') [*Iter sinense* 1914–1918 no. 11.428.] (W 1928/6071—lectotype).

18. **Mycomicrothelia modesta** (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia modesta Müll. Arg. in *Bull. Herb. Boissier* **2**: 93 (1894).

Fig. 35A–C.

Ascomata arising singly, scattered, colonies olivaceous, not clearly delimited, subperidermal, the surface raised to form low hemispherical projections; individual ascomata dimidiate, applanate, (200–)250–300 μm diam, 70–90(–100) μm tall, black, basal fringe scarcely extending beyond the limits of the ascomata and to only about 25 μm wide, fringe with a purplish tinge, giving a violet colouration in parts with iodine, ostiole depressed and 40–60 μm wide; involucrellum dark reddish brown becoming olivaceous in potassium hydroxide, 20–35μm thick, consisting of host cells intermixed with fungal hyphae, hyphae spreading irregularly, mainly 2–3 μm thick, reddish brown but becoming somewhat olivaceous in potassium hydroxide, uneven, ± smooth-walled; exciple poorly developed to ± absent, represented only by a few interwoven reddish brown hyphae; base of the ascomatal cavity not differentiated from the generative tissues; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, branched and sometimes anastomosed, regularly septate, 2–3 μm thick. *Asci* arising mainly in

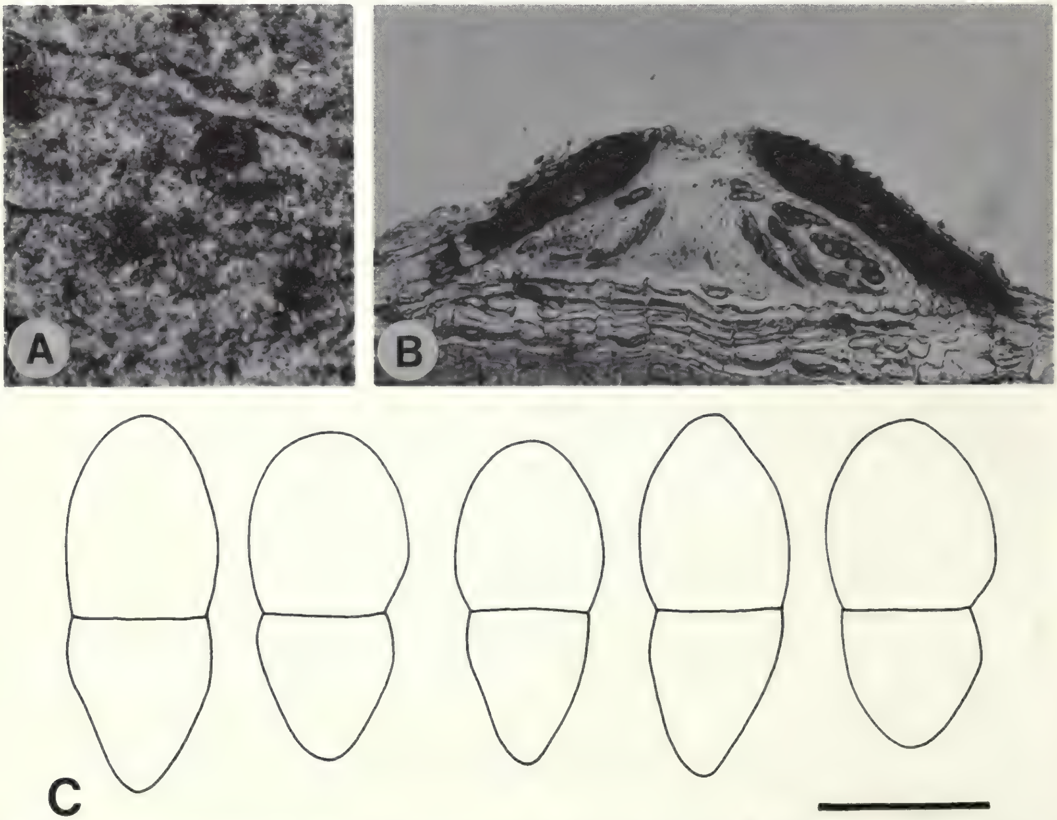

Fig. 35 *Mycomicrothelia modesta* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

the angles of the ascomata and orientated towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a well-developed internal apical beak when young, 63–67 × 17–20 μm, 8-spored. *Ascospores* irregularly distichously arranged in the asci, broadly ellipsoid to soleiform, 1-septate, somewhat constricted at the septum, the lower cell slightly smaller, broadly rounded at the apex and rounded to slightly attenuated at the base, olive brown, verruculose, with a distinct gelatinous sheath 1–1·5 μm thick in potassium hydroxide, (17·5–)19–22(–23) × (8–)8·5–10(–10·5) μm.

Anamorph: Unknown.

Host: Unidentified bark. Apparently not lichenized.

Distribution: Mexico. Known only from the original collection.

Observations: The ascospore size of this species recalls *Mycomicrothelia thelena* but the ascomata are smaller in diameter and also shorter in *M. modesta*. Furthermore, no whitish thallus is formed in the present species while one is typical of *M. thelena*. The ascospores of *M. modesta* are too long and broad for *M. captiosa*, and most strongly recall those of *M. confluens*; in the latter species, however, the ascomata are always grouped together on a well-developed basal fringe, while in *M. modesta* they arise singly and the basal fringe is rudimentary.

Specimen: **Mexico:** Jalisco, 1892, *J. W. Eckfeldt* 182 (G—holotype).

19. **Mycomicrothelia nonensis** (Stirton) D. Hawksw., **comb. nov.**

Verrucaria nonensis Stirton in *Proc. Phil. Soc. Glasgow* **11**: 320 (1879).
Microthelia nonensis (Stirton) Zahlbr., *Cat. Lich. Univ.* **1**: 264 (1921).

Fig. 36A–C.

Ascomata arising singly, rather evenly scattered over whitish areas of the bark, sometimes delimited, immersed, forming low hemispherical projections; individual ascomata dimidiate,

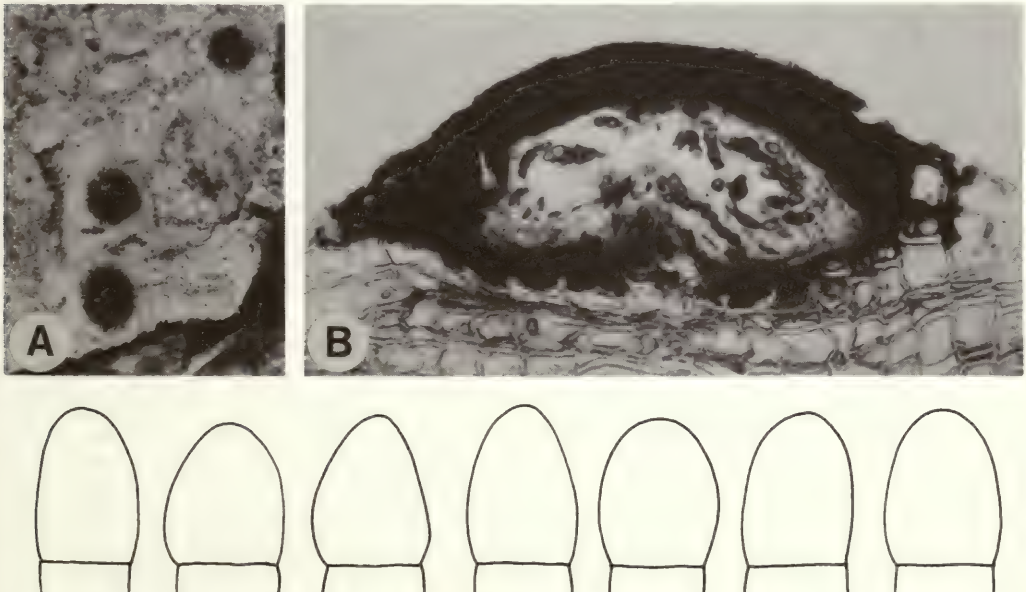

Fig. 36 *Mycomicrothelia nonensis* (BM—isotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

applanate at the base, 200–350 μm diam, 120–150 tall, basal fringe ± absent, ostiole depressed, 25–30 μm diam, black; involucrellum dark brown to dark reddish brown, becoming somewhat olivaceous in potassium hydroxide, mainly 30–40 μm thick, consisting of host tissue intermixed with fungal hyphae 3–3·5 μm thick, reddish brown, smooth-walled, between the host cells and also penetrating the lumina of the bark cells which become ± completely occluded; basal layer similar in structure, irregular in development, mainly 10–20 μm thick; exciple composed of subhyaline hyphae 2–2·5 μm thick, forming a layer 10–15 μm thick; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, septate, filiform, branched and anastomosing, 1.5–2 μm thick. *Asci* arising from the base and angles of the ascomatal cavity, oriented towards the ostiole, elongate-clavate, short-stalked, bitunicate, 50–60 × 8–15 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, 1-septate, constricted at the septum, the lower cells generally somewhat smaller, apices rounded to slightly attenuated, olivaceous brown, almost smooth to distinctly verruculose, with a thin gelatinous sheath to 1·5 μm thick in potassium hydroxide, (14–)15·5–17·5 × (6–)6·5–7·5 μm.

Anamorph: Unknown.

Host: Unidentified bark. Possibly lichenized with *Trentepohlia*, but no algal cells evident in vertical sections.

Distribution: India (Kerala).

Observations: This species recalls *Mycomicrothelia minutula* (p. 102) from which it can be distinguished by the larger ascomata and longer ascospores.

Specimens: **India:** Kerala, Nilghiri Hills ['Neilgherrie Mts'], *G. Watt* (BM—isotype of *Verrucaria nonensis*); loc. cit., *G. Watt* (BM, together with isotype of *V. clavaeformis*).

20. **Mycomicrothelia obovata** (Stirton) D. Hawksw., **comb. nov.**

Verrucaria obovata Stirton in *Trans. Proc. R. Soc. Victoria* **17**: 74 (1881).
Pyrenula obovata (Stirton) Shirley, *Lich. Fl. Queensl.* **4**: 176 (1890).
Microthelia obovata (Stirton) Müll. Arg. in *Rep. Austral. Soc. Advmt. Sci.* **6**: 454 (1895).
Microthelia alba Müll. Arg. in *Rep. Austral. Soc. Advmt. Sci.* **6**: 455 (1895).
Microthelia brisbanensis Müll. Arg. in *Rep. Austral. Soc. Advmt. Sci.* **6**: 455 (1895).

Figs 37A–D, 38A–C.

Ascomata arising singly, on a pinkish-white area of bark, thallus endophloeodal, delimited, immersed, the outer bark layers being raised to form hemispherical projections; individual ascomata dimidiate, base applanate, (250–)300–400 μm diam, (175–)200–300 μm tall, basal fringe not or scarcely extending, ostiole depressed, black; involucrellum dark reddish brown, becoming olivaceous in potassium hydroxide, mainly 45–60 μm thick, consisting of host tissue intermixed with fungal hyphae, hyphae irregularly orientated, mainly 2–2·5 μm thick, red brown, uneven, not distinctly verruculose, with tooth-like haustoria 0·5–1·5 μm thick often projecting into the lumina of the bark cells which may become occluded; basal tissue of the ascomata subhyaline, sometimes with a few dark red brown hyphae, forming a poorly defined layer 5–10 μm thick; centrum not turning blue with iodine. *Pseudoparaphyses* cellular, persistent, branched and anastomosing, 1·5–2·5(–3·5) μm thick. *Asci* arising from the base of the ascomata and the angle formed with the involucrellum, ± vertical to radially inclined, elongate-clavate, bitunicate, (65–)75–90 × 20–30 μm, 8-spored. *Ascospores* distichously arranged in the asci, broadly soleiform to broadly ellipsoid, 1–3 septate, slightly constricted at the median septum, upper cell tending to be the larger, the apices rounded, brown, coarsely verruculose, with a gelatinous sheath 1·5–2 μm thick, (21–)22–28(–30) × (8·5–)9–11(–12) μm.

Anamorph: Unknown.

Host: On unidentified bark. Probably lichenized with *Trentepohlia*, but fresh material is needed for confirmation.

Distribution: Australia (Queensland). No recent collections seen.

Observations: This species shows some similarity to the South American *Mycomicrothelia thelena* (p. 112), from which it can be distinguished by the larger ascospores which also finally

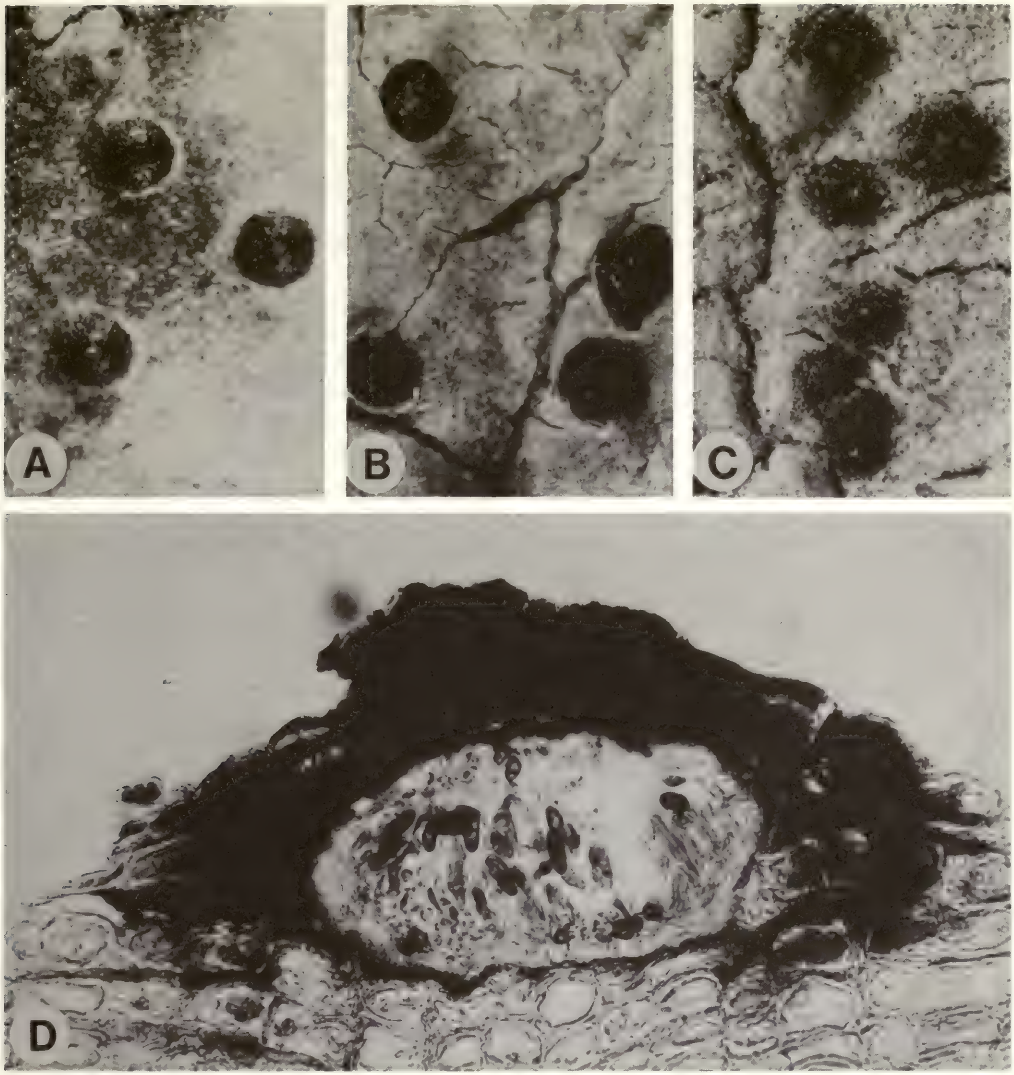

Fig. 37 *Mycomicrothelia obovata.* **A–C**, Surface view, × 20; **A**, BM—holotype of *Verrucaria obovata*; **B**, G—holotype of *Microthelia brisbanensis*; **C**, G—holotype of *M. alba*. **D**, Vertical section of ascoma (material as **C**), × 250.

become 3-septate, and also to *M. hemisphaerica* (p. 86) from Costa Rica which differs in the relatively narrower ascospores that rarely exceed 9 μm in width.

No type material of *Verrucaria obovata* was located by Rogers (1982: 509), evidently because the BM collection was then on loan.

Specimens: **Australia:** Queensland, Brisbane, *F. M. Bailey* 125 (BM—holotype of *Verrucaria obovata*; BM—isotype); loc. cit., 1891, *F. M. Bailey* (G—holotype of *Microthelia brisbanensis*); Queensland, 1887, *C. Knight* (G—holotype of *M. alba*; also other collections sub *M. queenslandica*, see p. 161).

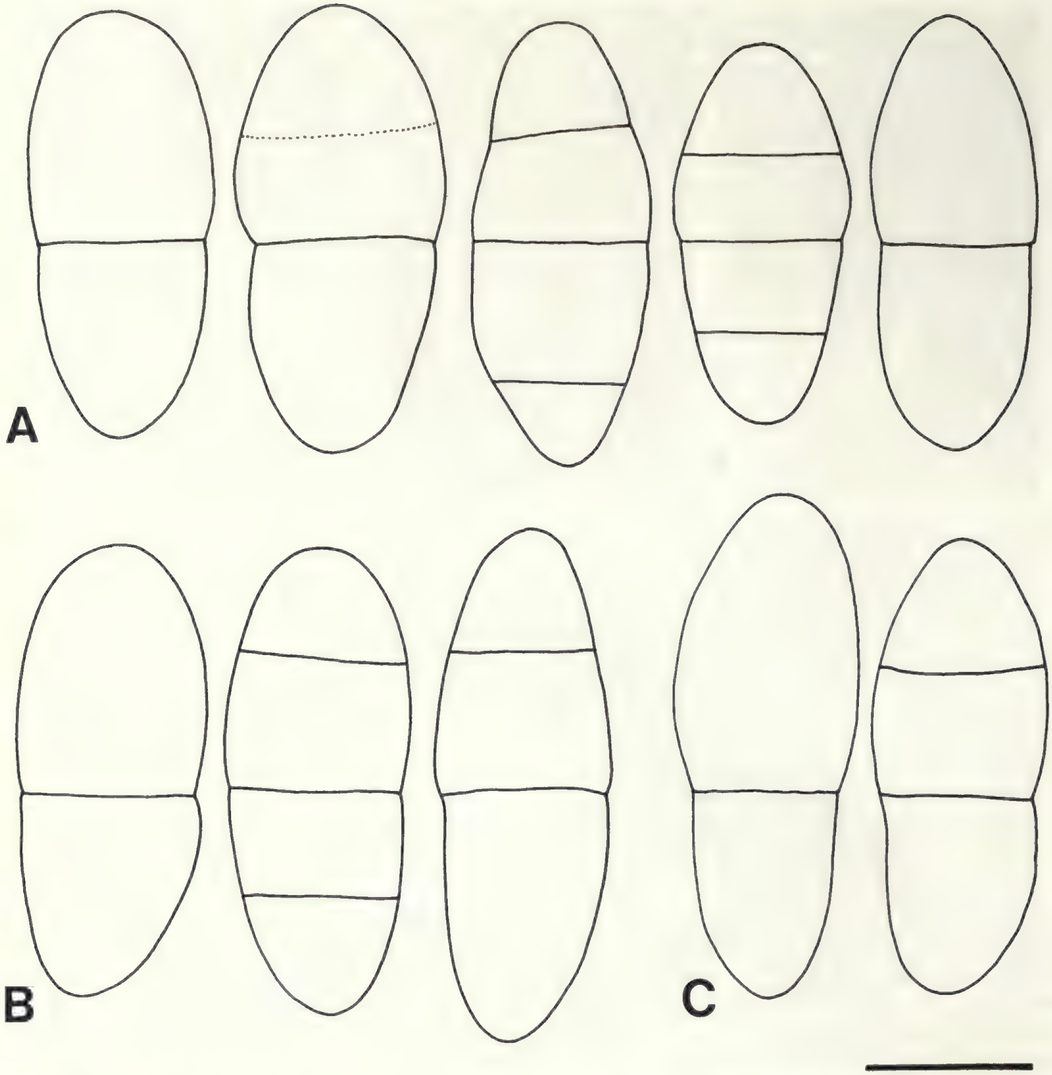

Fig. 38 *Mycomicrothelia obovata* ascospore outlines. **A**, BM—holotype of *Verrucaria obovata*. **B**, G—holotype of *Microthelia brisbanensis*. **C**, G—holotype of *M. alba*. Scale = 10 μm.

21. **Mycomicrothelia pachnea** (Körber) D. Hawksw., **comb. nov.**

Microthelia pachnea Körber, *Parerg. Lich.*: 398 (1865).
Amphisphaeria pachnea (Körber) Rehm in *Annls mycol.* **4**: 264 (1906).

Fig. 39A–C.

Ascomata arising singly, scattered over whitish areas of bark which are not delimited by a black line, immersed, subepidermal, the epidermis raised to form hemisphaerical projections, only the ostiole exposed; individual ascomata dimidiate, applanate, 200–300 μm diam, 100–120 μm tall, basal fringe scarcely extending, ostiole depressed, black; involucrellum dark reddish brown, becoming olivaceous in potassium hydroxide, mainly 15–25 μm thick, consisting of host tissue intermixed with fungal hyphae, hyphae irregularly radially orientated, 2·5–4(–5) μm thick, red brown, becoming olivaceous in potassium hydroxide, uneven, verruculose; basal tissue of the ascomata subhyaline, not differentiated from the generative tissues; exciple

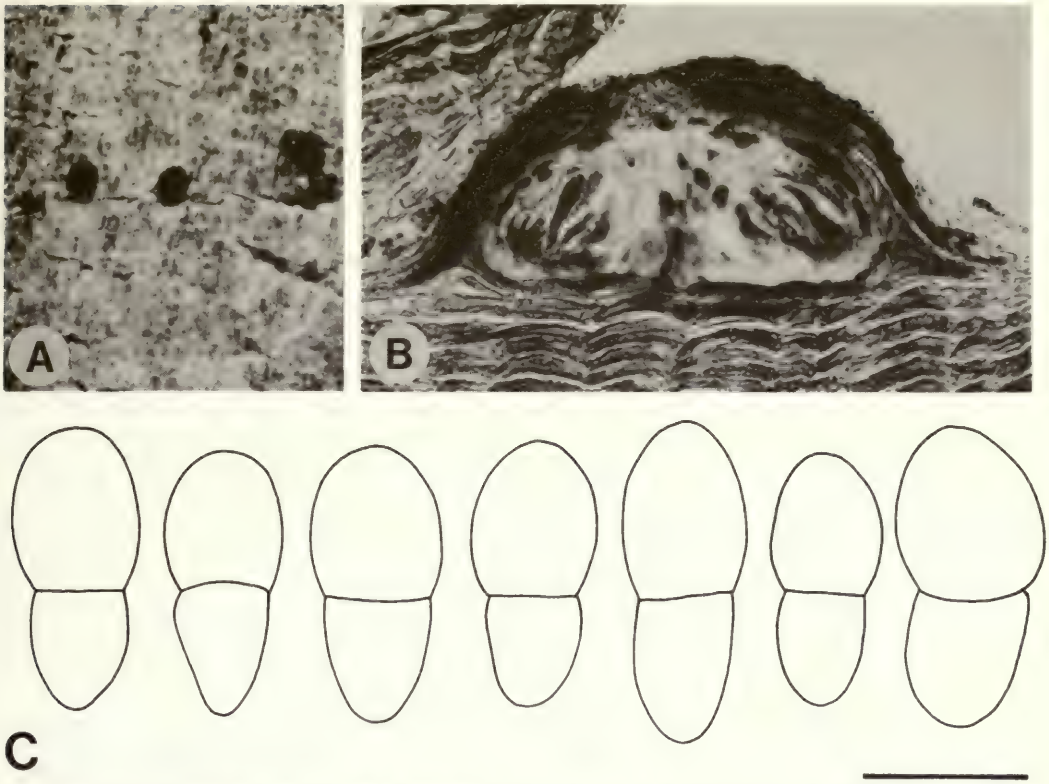

Fig. 39 *Mycomicrothelia pachnea* (L 910.195-404—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

composed of 3–4 layers of subhyaline interwoven hyphae *c.* 2 μm thick forming a layer 5–10 μm thick; centrum not reacting with iodine. *Pseudoparaphyses* cellular, persistent, numerous, filiform, septate, branched and anastomosing, 2–3 μm thick. *Asci* arising from the tissue lining the base of the ascomata and especially from the angle formed with the involucrellum, vertical to radially inclined, elongate-clavate, without a distinct stalk, bitunicate, with a squared internal apical indentation, when mature 65–75 × 15–18 μm, 8-spored. *Ascospores* overlapping distichous in the asci, soleiform, 1-septate, markedly constricted at the septum, the upper cell larger, broader and rounded, the lower smaller, narrower and sometimes more attenuated, dark brown, distinctly verruculose, with a gelatinous sheath 1–2 μm thick, (15–)16–18 × (6·5–)7–8(–9) μm.

Anamorph: Unknown.

Host: On 'Tannenrinde' (i.e. *Abies* bark) and *Quercus*. Rehm (1906: 264) and Keissler (1936: 31) also mention an occurrence on *Populus*, but I have not seen the material on which these reports are based. Keissler evidently considered this species to be lichenized with *Trentepohlia*. In the type collection a few algae were found in vertical section on the surface of the bark and also within the upper layers of bark cells, but these were sporadic in occurrence and no well-defined thallus is formed. The species is best regarded as either non- or facultatively lichenized as most of its nutrients may be presumed to originate in the host tissues in which it is immersed.

Distribution: Austria, Spain, and possibly also Germany.

Observations: Mycomicrothelia pachnea has ascospores which have the apices generally broadly rounded. This character serves to distinguish this species from other members of the genus with rather similarly sized ascospores, including *M. confusa* which also grows in Europe.

Specimens: **Austria:** Kremsmünster, Teufelsleithen, 27 September 1856, *I. S. Pötsch* (L 910.195-404—holotype of *Microthelia pachnea*; L-910.195-406—isotype); Kremsmünster, Zürmwenigrun [?], 11 November 1857, *I. S. Potsch* (L-910.195-405). — **Spain:** Pais Vasco, Vizcaya, Gernica, on *Quercus robur*, 5 January 1983, *B. Aguirre & G. Renobales* (IMI 295846).

22. **Mycomicrothelia socialis** (Zahlbr.) D. Hawksw., **comb. nov.**

Microthelia socialis Zahlbr. in *Mycologia* **22**: 69 (1930).

Fig. 40A–E.

Ascomata arising in small groups of 2–6 or more rarely entirely alone, scattered over the surface of the bark which becomes whitish-grey in the herbarium but is reportedly 'roseo-albido' when fresher, colonies not delimited by a black line, immersed, subepidermal, the epidermal layers raised to form low hemispherical projections, only the ostiole exposed; individual ascomata dimidiate, (100–)150–200(–250) μm diam, 80–120 μm tall, basal fringe well-developed forming an ellipsoidal ring to 100 μm wide which is dark grey to almost black; ostiole slightly depressed, black; involucrellum dark brown, becoming olivaceous brown to greenish brown in potassium hydroxide, 10–15(–20) μm thick, consisting of host tissue intermixed with fungal hyphae, the hyphae spreading radially, much branched, 2–3·5 μm thick, uneven, smooth-walled, branching between the host cells and forcing them apart; exciple 7–15 μm thick, composed of 3–6 layers of hyphae 2–3·5 μm wide, textura intricata, compacted, brown to dark brown but becoming rather olivaceous in potassium hydroxide, pale brown and more irregular at the base; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, abundant, many-septate, irregularly branched and anastomosing, 1·5–2·5 μm thick. *Asci* arising from the base of the ascomatal locule, ± vertically orientated in the centre but sloping towards the ostiole from towards the

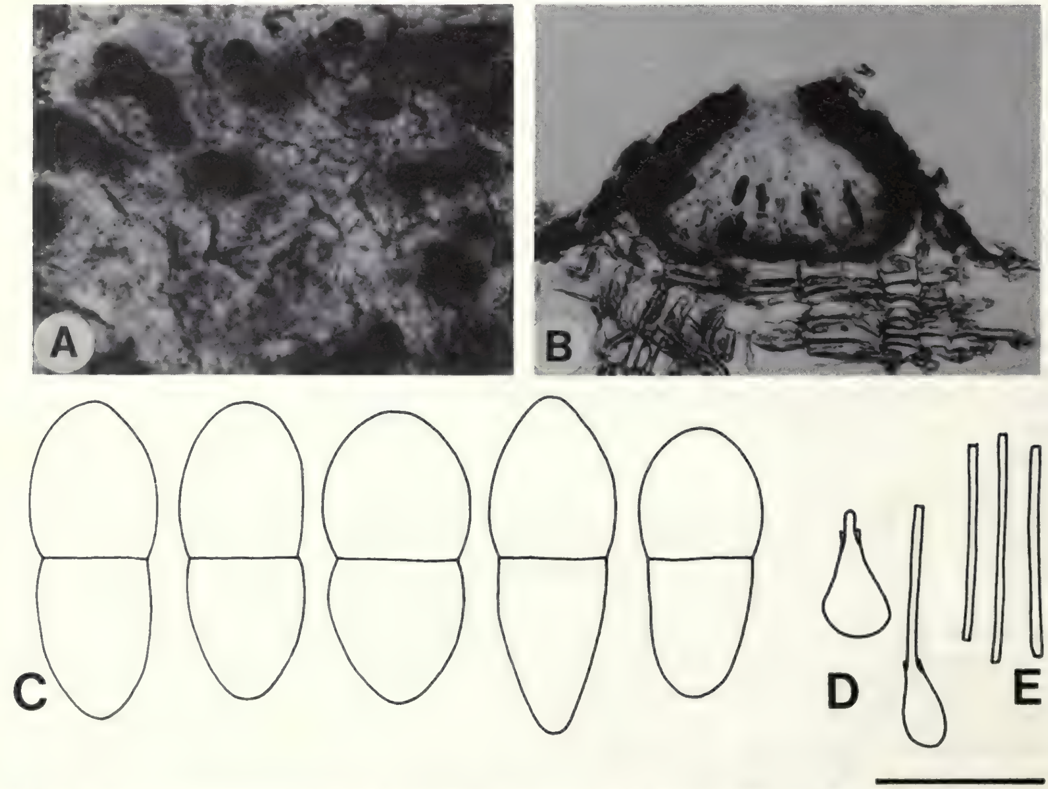

Fig. 40 *Mycomicrothelia socialis* (W 1925/9360—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines. **D**, Conidiogenous cells. **E**, Conidia. Scale **C–E** = 10 μm.

sides, elongate-clavate, short-stalked, bitunicate, with a somewhat attenuated thickened apex with a squared internal apical beak, 45–60 × 15–24 μm, 8-spored. *Ascospores* irregularly distichously arranged in the asci, ellipsoid, 1-septate, slightly constricted at the septum, cells almost equal in length but the lower often slightly narrower, rounded at the apices, brown, almost smooth but at high magnifications seen to have a delicate verruculose ornamentation, with a thin gelatinous sheath (1–1·5 μm thick in potassium hydroxide), 15–20 × 6–9 μm.

Anamorph: On one part of the type specimen minute black pycnidia 50–75 μm diam are intermixed with the ascomata. It is conceivable that these are an anamorph of this species, but the possibility that they are a fortuitously present coelomycete cannot be excluded. Further, the pycnidia have almost pseudoparenchymatous rather than hyphal walls. The conidiogenous cells are short-ampulliform, hyaline, mainly 7–10 × 2·5–3·5 μm, phialidic, and produce numerous bacilliform conidia which are hyaline and 12–15 × 0·5–1(–1·5) μm.

Host: Unidentified bark, perhaps at least partially lichenized according to the original description, but no algae definitely associated with the hyphae of the fungus were noted in vertical sections.

Distribution: West Indies (Puerto Rico). Known only from the original collection.

Observations: This species is rather similar to *Mycomicrothelia wallrothii* in many respects, especially in the structure of the ascomata, their dark fringe, and ascospore size. It is retained here as a separate species because of the gregarious nature of the ascomata which also tend to be smaller in both overall dimensions and thickness of the involucrellum and ascomatal cavity wall layers. The host of *M. socialis* is not *Betula*, and the pycnidia associated with *M. socialis* are quite different from the anamorph of *M. wallrothii*.

Specimen: **West Indies:** Puerto Rico, Yauco, open hill top, on bark, 29 December 1915, *B. Fink* 1459a (W 1925/9360—holotype).

23. **Mycomicrothelia subfallens** (Müll. Arg.) D. Hawksw., **comb. nov.**

Microthelia subfallens Müll. Arg. in *Bot. Jb.* **6**: 416 (1885).

Fig. 41A–C.

Ascomata arising singly, scattered, colonies whitish to pale rose, forming mosaics delimited by black lines 50–150 μm thick, subepidermal, the epidermal layers raised very slightly to form low hemispherical projections; individual ascomata 150–250(–300) μm diam, 60–100 μm tall, dimidiate, black, with a basal fringe to 50 μm thick, ostiole depressed; involucrellum reddish brown, becoming deep olivaceous brown in potassium hydroxide and then with a purplish tinge, mainly 25–50 μm thick, consisting of host cells intermixed with fungal hyphae, hyphae irregularly orientated but spreading radially at the base, 2–3·5 μm diam, sometimes uneven in diameter, ± smooth-walled, between and sometimes entering the host cells which become occluded; exciple poorly delimited, comprising a variable number of layers of hyphae which are subhyaline except in the vicinity of the ostiole where they are reddish brown (textura intricata); the base not clearly delimited from the ascogenous layer, subhyaline; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, rather sparsely branched and occasionally anastomosing, numerous, septate, 1·5–2 μm thick. *Asci* arising from the base of the ascomatal cavity, tending to be inclined towards the ostiole, elongate-clavate, short-stalked, bitunicate, with a narrow internal apical beak, 50–65 × 12–14 μm, 8-spored. *Ascospores* irregularly distichously arranged in the asci, ellipsoid, 1-septate, constricted at the septum, the lower cell consistently smaller, rounded at the apices, golden brown, verruculose, gelatinous sheath distinct and to 2 μm thick in potassium hydroxide, 13·5–16 × 6–7 μm.

Anamorph: Unknown.

Host: Bark of unidentified tree or shrub. The mosaic-like appearance suggests that the species may be lichenized, but no algae were seen to be intimately associated with the ascomata in the sections prepared.

Distribution: Cuba. Known only from the original collection.

Observations: This species is very close to *Mycomicrothelia minutula* and should perhaps be

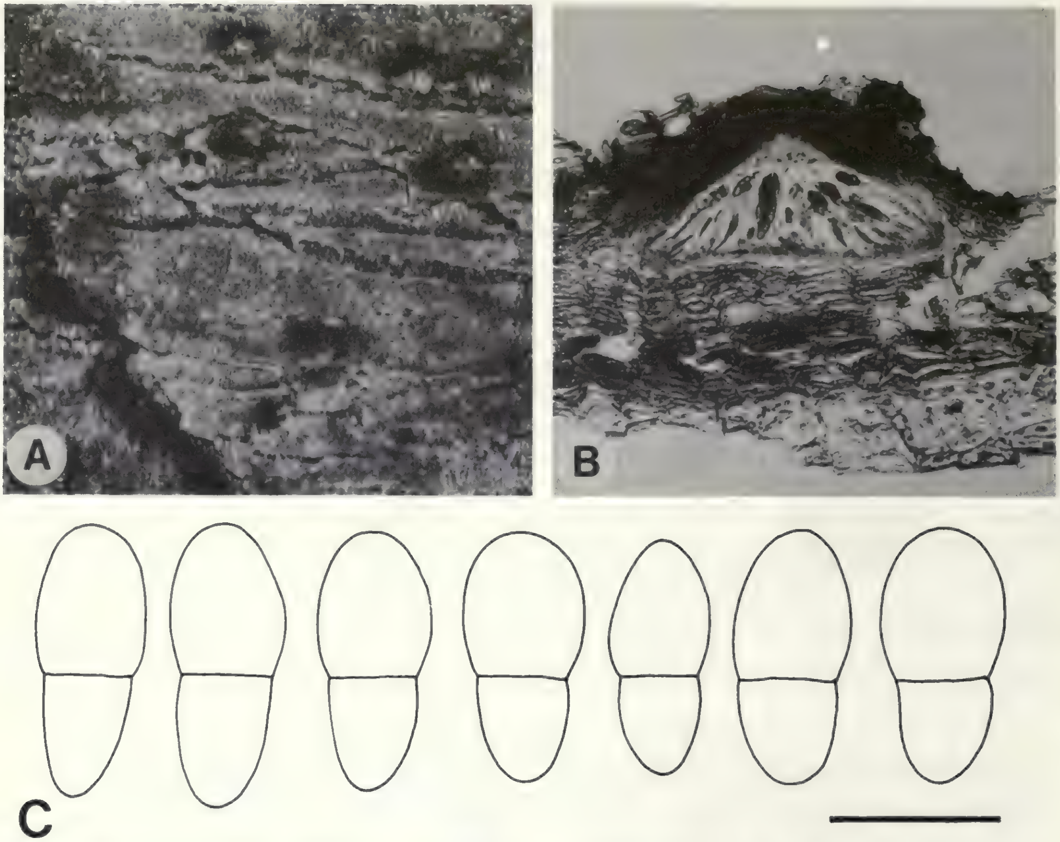

Fig. 41 *Mycomicrothelia subfallens* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

united with it. The two are retained here, however, in view of the more deeply immersed ascomata of *M. subfallens* which also have a much better developed fringe, but future collections may show that this is not a valid specific criterion.

In the original account the ascospores were given as 11–14 × 4–5 μm wide but this does not accord with my observations; Müller presumably examined immature ascospores.

Specimen: **Cuba:** *sine loc., C. Wright* [*Verr. cub.* exs. *5*] (G—holotype).

24. **Mycomicrothelia thelena** (Ach.) D. Hawksw., **comb. nov.**

Verrucaria thelena Ach., *Syn. Lich.*: 92 (1814).
Microthelia thelena (Ach.) Trevisan, *Consp. Verruc.*: 10 (1860).
Microthelia thelena var. *subtriseptata* Vainio in *Acta Soc. Fauna Fl. fenn.* **7** (2): 232 (1890).
Microthelia leucothallina Vainio in *Ann. Acad. sci. fenn.* A, **6** (7): 210 (1915).
Microthelia albidella Müll. Arg. in *Flora, Jena* **66**: 272 (1883).

Figs 42A–B, 43A–D.

Ascomata arising singly, occasionally becoming confluent, scattered over areas of the bark which are creamy or whitish or not discoloured in any way, often delimited by a black line, immersed, subepidermal, the epidermis raised to form hemispherical projections; individual ascomata dimidiate, applanate, (250–)300–400(–450) μm diam, 100–250 μm tall, basal fringe variable in development ± absent or to *c.* 70 μm wide, ostiole depressed, black; involucrellum dark reddish brown, ± unchanged in potassium hydroxide, very variable in thickness, mainly

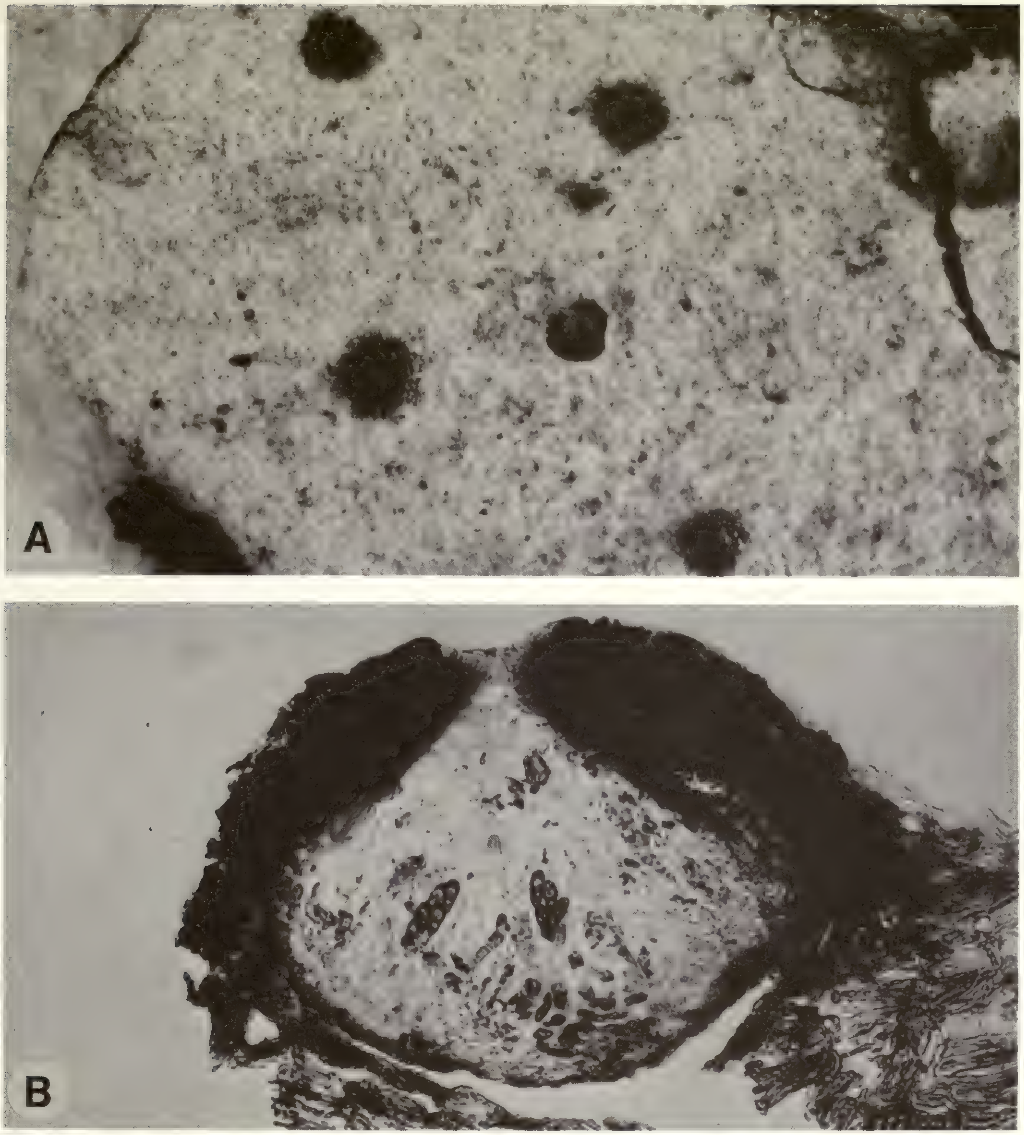

Fig. 42 *Mycomicrothelia thelena*. **A**, Surface view (TUR 33038—holotype of *Microthelia leucothallina*), × 20. **B**, Vertical section of ascoma (G—holotype of *M. albidella*), × 250.

30–70 μm thick, consisting of host tissue intermixed with fungal hyphae, hyphae 2–3·5 μm thick, red brown but becoming somewhat olivaceous in potassium hydroxide, uneven, smooth-walled; basal tissue of the ascomata either subhyaline and not differentiated from the generative tissues or similar to the involucrellum but not exceeding *c.* 10 μm thick; exciple composed of 2–4 layers of subhyaline interwoven hyphae forming a layer 5–15 μm thick; centrum not reacting with iodine. *Pseudoparaphyses* cellular, persistent, numerous, occasionally septate, filiform, branched and anastomosing, mainly (1·5–)2–3 μm thick. *Asci* arising from the tissue lining the base of the ascomata, mainly vertically inclined except towards the margins, clavate, short-stalked, bitunicate, without a well-marked apical indentation when mature, 80–90(–100) × (23–)26–31 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, 1-septate, slightly constricted at the septa, the upper cell usually slightly larger, cells more rarely ± equal in size,

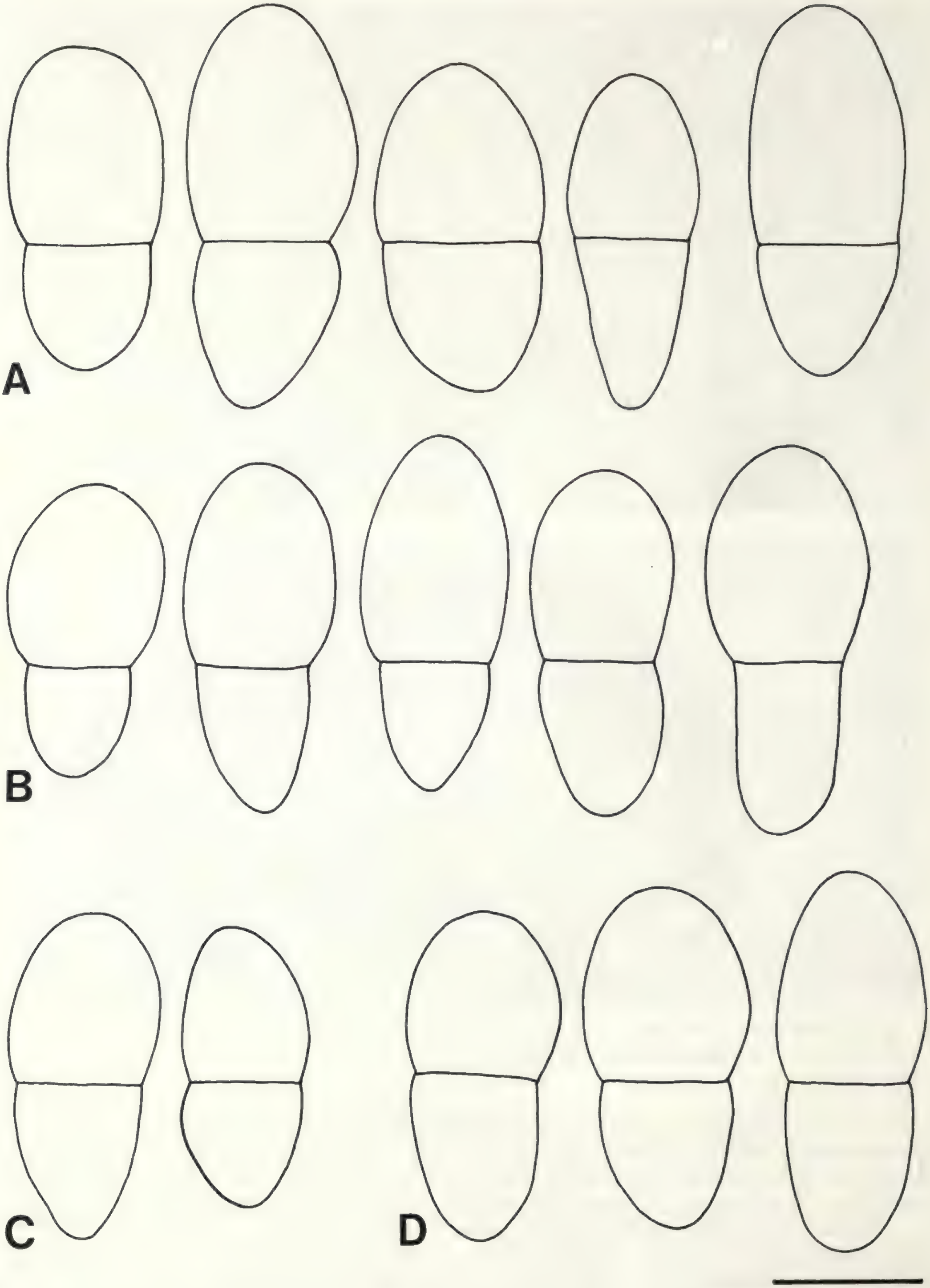

Fig. 43 *Mycomicrothelia thelena* ascospore outlines. **A**, H-NYL 705—ex-holotype of *Verrucaria thelena*. **B**, TUR 33038—holotype of *Microthelia leucothallina*. **C**, BM—isotype of *M. thelena* var. *subtriseptata*. **D**, G—holotype of *M. albidella*. Scale = 10 μm.

rounded at the apices, deep golden brown, distinctly verruculose, with a thin gelatinous sheath 1–1·5(–2) μm thick in potassium hydroxide, (17·5–)21–24(–26) × (7·5–)9–11·5(–13) μm.

Anamorph: Unknown.

Illustrations: Fée, *Essai Crypt.*: tab. 22 fig. 5a–c (1825) [not tab. 1 fig. 11!].—Morgan-Jones in *Lichenologist* **5**: 276 fig. 3 (1972).

Exsiccata: Vainio, *Lich. Brasil* 715 (sub *Microthelia thelena* var. *subtriseptata*; BM—isotype).

Host: On bark of various trees. Apparently lichenized with *Trentepohlia*.

Distribution: Tropical Central and South America. Probably widespread in this region. I have seen specimens from Brazil, Uruguay, and the West Indies.

Observations: This species is separated from *Mycomicrothelia conothelena* (p. 81) by the involucrellum which is less sharply conical, consisting of a much higher proportion of periderm cells from the host, and not markedly carbonaceous; in addition the ascospores of *M. conothelena* rarely exceed 21 μm in length. *M. obovata* (p. 106) produces ascospores which are rather similar in size, but 3-septate ascospores are often formed and differ somewhat in shape; I was at first inclined to unite these two species, but in view of the geographical separation and differences in the ascospores consider that it is more appropriate to retain them as distinct for the time being. It should be noted that no truly 3-septate ascospores were seen by me in *Microthelia thelena* var. *subtriseptata*.

Acharius (loc. cit.) gave the original habitat of *Verrucaria thelena* as 'ad corticem *Bonplandiae trifoliatae*'. There are now two specimens under this epithet in Acharius' herbarium on *Bonplandia trifoliata* (H-ACH 692B) and on *Cinchona* (H-ACH 692A). No ascospores were found in single ascomata sent from each of these by Mr O. Vitikainen, but I was able to find ascospores in a fragment in Nylander's herbarium which had apparently come from Acharius' material (H-NYL 705) which was labelled simply 'Amer. merid.'. As Nylander evidently considered this to be from the type of Acharius' name, I am assuming that it was from the *Bonplandia* specimen and have applied this species name here in the sense of this fragment.

When introducing the name *Microthelia leucothallina*, Vainio (loc. cit.) indicated that the spores were uniseriately arranged in the asci; this was not confirmed in slides made by me, and it seems probable that his observation was based on discharging asci. Rather few ascospores could be found in the type material of *M. albidella* but those seen clearly fell within the range for the species.

Additional specimens: **South America:** 'Amer. meridion.' (H-ACH 692B [slide H-NYL 705]—holotype of *Verrucaria thelena*). – **Brazil:** Apiahy, July 1879, *Puiggari* 349 (G—holotype of *Microthelia albidella*). – **Uruguay:** Maldonado-Cerro Pan de Azucar, on *Sapium*, 29 February 1948, *H. Osorio* 1525 (CAN(L)). – **West Indies:** 'Insulis Danicis', 'ad corticem arbori', 1905–06, *F. Boergesen* (TUR 33038 [hb. Vainio 32469]—holotype of *M. leucothallina*).

25. **Mycomicrothelia wallrothii** (Hepp) D. Hawksw., *in* Hawksworth *et al.* in *Lichenologist* **12**: 107 (1980).

Pyrenula wallrothii Hepp, *Flecht. Eur.* exs. 709 (1860).
Microthelia wallrothii (Hepp) Rehm in *Hedwigia* **18**: 163 (1879).
Didymosphaeria wallrothii (Hepp) Rehm *in* Saccardo, *Syll. Fung.* **1**: 715 (1882).
Massariopsis wallrothii (Hepp) Rehm in *Annls mycol.* **4**: 270 (1906).
Verrucaria wallrothii (Hepp) Norrlin, *Bildr. Sydöstr. Tav. Fl.*: 195 (1870) [non vidi].
Microthelia betulina Lahm *in* Körber, *Parerg. Lich.*: 397 (1865).
Microthelia cinerella subvar. *betulina* (Lahm) Boistel, *Nouv. Fl. Lich.* **2**: 289 (1903).
Microthelia oblongata Müll. Arg. in *Flora, Jena* **68**: 332 (1885).
Pyrenula oblongata (Müll. Arg.) Willey, *Enum. Lich. New Bedford*: 39 (1892).
Microthelia betulina f. *populicola* Norman in *K. norske Vidensk. Selskr. Skr.* **5**: 374 (1868).

Figs 44A–B, 45A–F.

Ascomata arising singly, scattered over the surface of the bark which is not discoloured in any way, colonies not delimited, immersed, subepidermal, the epidermis raised to form hemispherical projections, only the ostiole exposed; individual ascomata dimidiate, 150–250(–300) μm

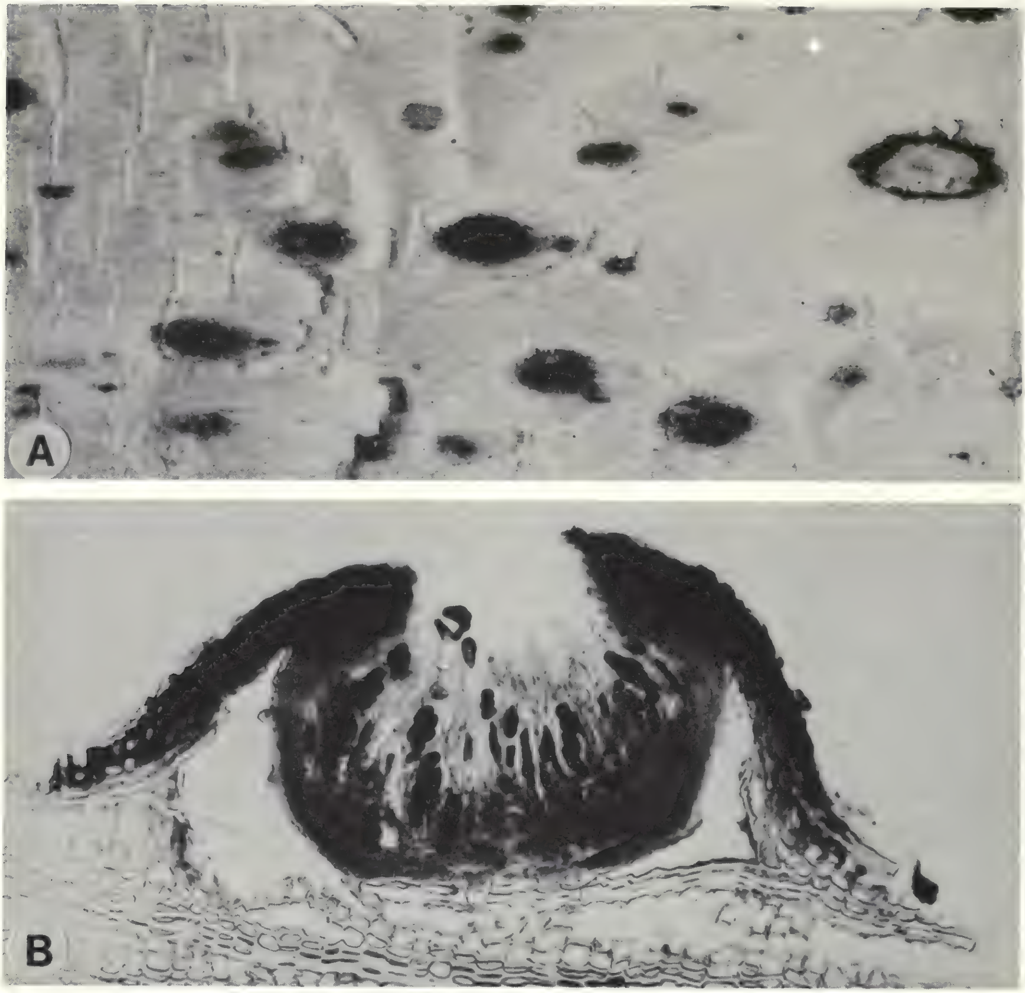

Fig. 44 *Mycomicrothelia wallrothii.* **A**, Surface view showing ascomata interspersed with pycnidia (G—holotype of *Microthelia oblongata*), × 20. **B**, Vertical section of ascoma (L 910.195-251—holotype of *M. betulina*), × 250.

diam, 120–160 μm tall, basal fringe well-developed forming an ellipsoid ring to 300 μm wide which is dark gray, ring olivaceous in potassium hydroxide, ostiole depressed, black; involucrellum dark brown, somewhat olivaceous in potassium hydroxide, mainly 20–30 μm thick, consisting of host tissue intermixed with fungal hyphae, hyphae irregularly radially orientated, 2–3 μm thick, uneven, entering and between cells of the host, ± smooth-walled; exciple 10–18 μm thick, composed of 4–8 layers of densely interwoven hyphae 2–3 μm wide (textura intricata), compacted, subhyaline close to the involucrellum but brown to dark brown for most of its length; centrum not reacting with iodine. *Pseudoparaphyses* cellular, persistent, numerous, septate, branched and anastomosing, 1–2 μm thick. *Asci* arising from the tissue lining the base of the ascomata, ± vertically orientated, elongate-clavate, short-stalked, bitunicate, with a shallow squared internal apical indentation, 35–60 × 14–16(–20) μm, 8-spored. *Ascospores* irregularly to distichously arranged in the asci, ellipsoid, 1-septate, not to slightly constricted at the septum, cells ± equal in size, the ends rather abruptly rounded and not attenuated, dark brown, indistinctly verruculose, with a gelatinous sheath *c.* 1 μm thick, (12–)14–18(–20) × 6–8(–8·5) μm.

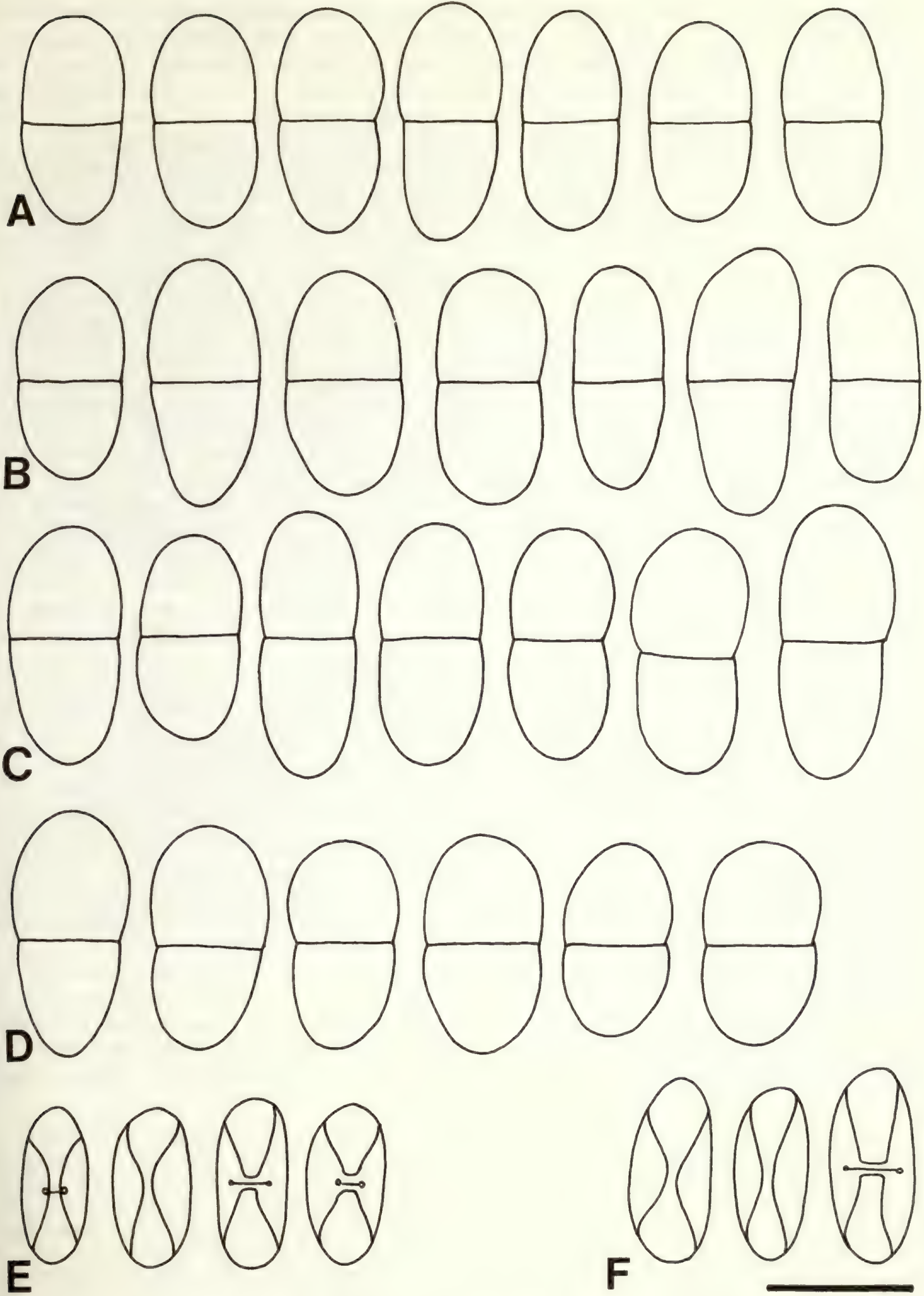

Fig. 45 *Mycomicrothelia wallrothii*. **A–D**, Ascospore outlines; **A**, K—isotype of *Pyrenula wallrothii*); **B**, L 910.195-251—holotype of *Microthelia betulina;* **C**, G—holotype of *M. oblongata*; **D**, O—lectotype of *M. betulina* f. *populicola*. **E–F**, Conidia (**E** material as **D**; **F** material as **A**). Scale = 10 μm.

Anamorph: Conidiomata intermixed with ascomata but sometimes present on their own, scattered, pycnidial, subepidermal, ovoid, vertically compressed, 50–100(–120) μm diam, black, sometimes with a small fringe; pycnidial wall similar in construction to that of the teleomorph, involucrellum-like structure hyphal, exciple-like structure hyphal to almost pseudoparenchymatous in parts, mainly 6–10 μm thick, olivaceous brown, hyphae 1·5–3 μm wide. *Conidiogenous cells* arising ± directly from the inner wall of the pycnidium, enteroblastic, acrogenous, short-ampulliform to almost doliiform, phialidic, proliferation not seen, hyaline, 4–8 × 3–5 μm. *Conidia* arising singly, not adhering in chains, ellipsoid to doliiform, walls unevenly thickened centrally and eventually becoming polarilocular with a distoseptum developing within the thickened tissue, apices rounded to somewhat truncated, without any basal frill, smooth-walled, lacking a gelatinous sheath, (9–)11–12·5(–14) × 4–6·5 μm.

Illustrations: Harris, *Mich. Bot.* **12**: 57 fig. 31 (1973). – Hepp, *Flecht. Eur.* exs. 709 (1860).

Exsiccata: Hepp, *Flecht. Eur.* 709 (sub *Pyrenula wallrothii*; K, L-910.195-370—isotypes).

Host: On bark of *Betula* species; exceptionally on *Populus*. Evidently not lichenized, although occasional algal cells fortuitously occur on or around the ascomata.

Distribution: A very widely distributed species in northern and central Europe and North America. I have examined material from the British Isles (anamorphs only), Germany, Norway, Switzerland, and the U.S.A. There are published reports at least from Canada (Bird et al. 1981), Denmark (Magnusson, 1944), France (Ozenda & Clauzade, 1970), Italy (Jatta, 1911), Poland (Nowak & Tobolewski, 1973), Romania (Moruzi et al., 1967), Sweden (Magnusson, 1944), and the U.S.S.R. (Kopaczevskaja et al., 1977). For further information on this speces in North America see Harris (1973: 27).

Observations: Hepp's exsiccatum included both the teleomorph and anamorph. Körber (1865: 297) mentions Hepp's exsiccatum in his discussion of *Microthelia betulina* but, as he did not definitely state that he accepted Hepp's name as a synonym, I consider that the epithet *'betulina'* is not illegitimate under Art. 63.1.

Harris (1973: 27) noted that the hyphae at the base of the ascomata of this species turned pale violet in iodine, but this appears to be a variable feature. *Microthelia oblongata*, which Harris separated by the lack of a violet reaction in iodine, is consequently not retained as a separate species here as it appears to agree in all other details with *M. wallrothii*; I did not obtain a violet reaction in the holotype of *M. betulina* or Hepp's exsiccatum.

The conidia of this species are highly characteristic and recall the macroconidia of *Eopyrenula leucoplaca* (Wallr.) R. C. Harris in various respects. The relationship of this species to *Mycomicrothelia* clearly merits more detailed study.

Keissler (1936: 39) gave the ascospore length as 10–17 μm, but mature ascospores were seen to be mainly 14–18 μm in length; it is conceivable that the lower figures were derived from conidia.

The material on *Populus* from Norway agrees in all details with that on *Betula*; although the conidia tended to be slightly smaller (9–12 × 4–6·5 μm) they have the same internal structure of *wallrothii* and come within the range of variation of the anamorph as on *Betula*. The name *'populicola'* does not appear on specimens on poplar from the type locality in O and TRH; that with a description in Norman's hand in O is selected as lectotype and includes both teleomorph and anamorph.

Specimens: **British Isles:** SCOTLAND: East Inverness, Strathfarrer Forest, on *Betula*, 27 May 1975, *B. J. Coppins* 2261 (E). – **Germany:** Munster, on *Betula*, *Lahm* (L 910.195-251—holotype of *Microthelia betulina*). – **Norway:** 'In Gildeskaal ad Skovvold', on *Populus*, *J. M. Norman* (O—lectotype of *M. betulina* f. *populicola*; TRH—isolectotype); Vegö, lanpliden, *J. M. Norman* (O); Helgo 'in Steigen ad Vasdalen', *J. M. Norman* (O); 'in Maalselom', *J. M. Norman* (O); Nasö, Holand, *J. M. Norman* (O). – **Switzerland:** Zurich, 'an Birkenrinde', *Hegetschweiler* [Hepp, *Flecht. Eur.* exs. 709] (K, L 910.195-370—isotypes of *Pyrenula wallrothii*). – **U.S.A.:** Massachusetts, New Bedford, on *Betula alba*, 1876, *Willey* (G—holotype of *M. oblongata*).

26. Mycomicrothelia willeyana (Müll. Arg.) D. Hawksw., comb. nov.

Microthelia willeyana Müll. Arg. in *Flora, Jena* **68**: 332 (1885).
Pyrenula willeyana (Müll. Arg.) Willey, *Enum. Lich. New Bedford*: 39 (1892).

Fig. 46A–D.

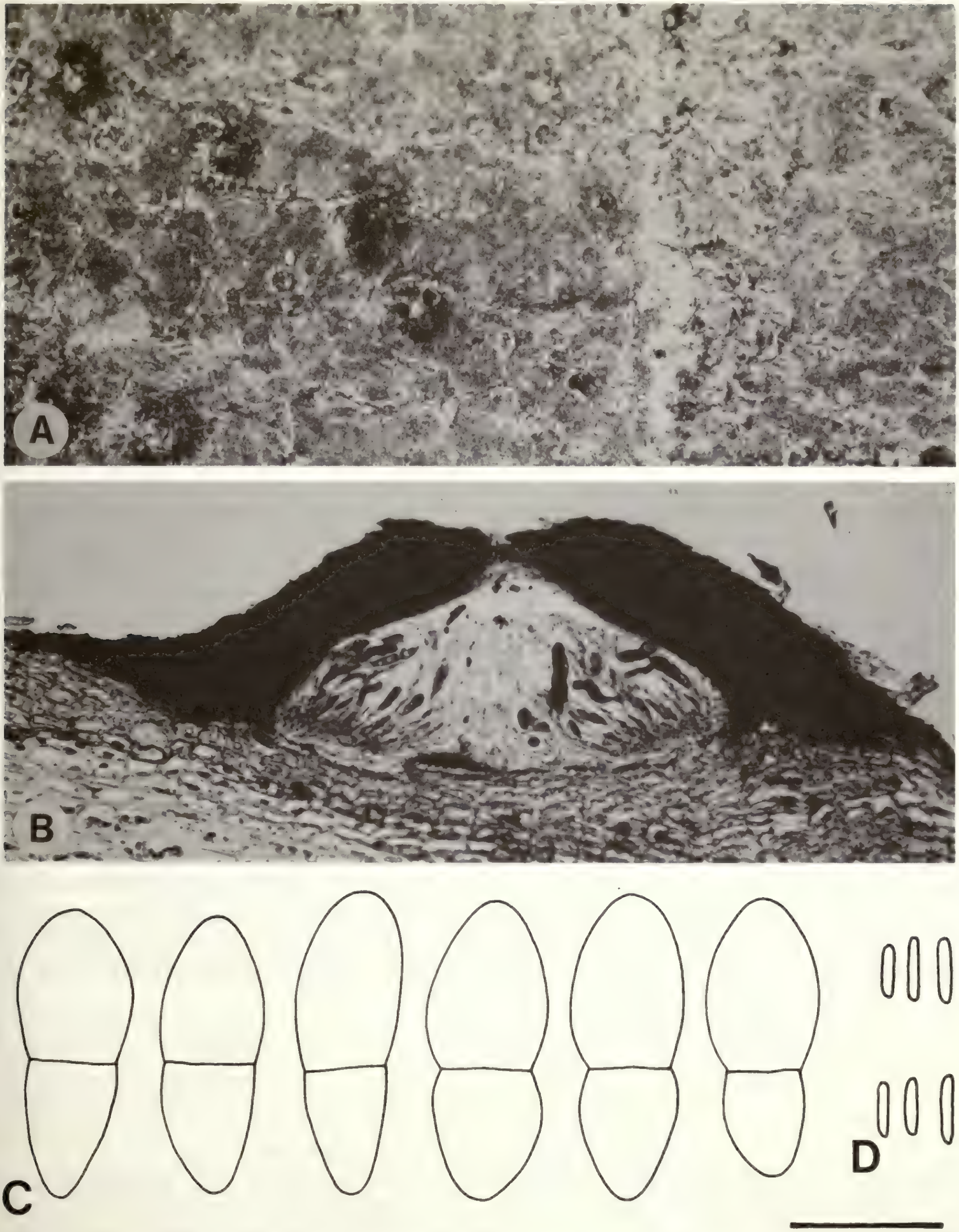

Fig. 46 *Mycomicrothelia willeyana* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines. **D**, Conidia. Scale **C–D** = 10 μm.

Ascomata mainly arising singly but sometimes 2–3 confluent at the margins, the bark not discoloured, margins between separate thalli of this species and also between it and adjacent crustose lichens marked by a black hyphal zone 200–300 μm wide, immersed, subepidermal, the epidermal layers raised to form low hemispherical projections, only the ostiole exposed; individual ascomata dimidiate, 200–300 μm diam, 100–150 μm tall, basal fringe distinct and 50–100 μm wide surrounding the ascomata, black, ostiole scarcely depressed but not protruding with the whitish centrum visible through it and mainly 30–50 μm wide; involucrellum dark reddish brown but becoming more olivaceous in potassium hydroxide, 40–60 μm thick, composed of host cells bound together by fungal hyphae, hyphae sometimes apparently penetrating the host cells which then become occluded, hyphae irregularly orientated but tending to be radially arranged, 2–3 μm thick, uneven, smooth-walled, dark olivaceous brown in potassium hydroxide, the involucrellum invaded by hyphae turning violet in iodine, host cells at the base of the exciple mainly 5–10 μm thick, composed of a varying number of layers of interwoven hyphae 2–3 μm thick forming a textura intricata, reddish brown but becoming olivaceous in potassium hydroxide, not continuing along the base of the locule which is scarcely differentiated from the generative tissues; centrum not turning blue in iodine. *Pseudoparaphyses* cellular, persistent, irregularly branched and anastomosed, septate, 1·5–2·5 μm thick. *Asci* arising from the base of the ascomatal cavity and especially from the basal angles of the ascomata, inclined towards the ostiole, subcylindrical to elongate-clavate, bitunicate, with a distinct internal apical beak when young, 50–65 × 10–12 μm, [4–?]8-spored. *Ascospores* distichously arranged in the asci to almost overlapping-monostichous, soleiform, 1-septate, strongly constricted at the septum, the lower cell consistently smaller, rounded to somewhat attenuated at the apices, olivaceous brown, verruculose, with a thin gelatinous sheath to about 1·5 μm thick in potassium hydroxide, 17–20(–21) × 7–8(–9) μm.

Anamorph: Conidiomata scattered amongst the ascomata but most abundant near the margins of the colonies where ascomata are absent, pycnidial, 50–75 μm diam, black; pycnidial wall similar in structure to the walls of the ascomata, formed of interwoven reddish brown hyphae becoming olivaceous in potassium hydroxide, hyphae 2–3 μm thick, rather uneven. *Conidiogenous cells* arising ± directly from the pycnidial wall, elongate-ampulliform to subcylindrical, enteroblastic, phialidic, acrogenous, hyaline, mainly 4–8 × 1·5–2 μm. *Conidia* arising singly, not adhering in chains, bacilliform to narrowly fusiform, simple, slightly more rounded at the apex than at the base, hyaline, 3–4 × 1–1·5 μm.

Host: Fraxinus bark. Probably lichenized with endophloeodal *Trentepohlia*.

Distribution: U.S.A. (Massachusetts). Known only from the original collection.

Observations: The superficial appearance of this species strongly recalls *Arthopyrenia lapponina* Anzi, but the brown spores (while still within the asci) and shorter conidia exclude that possibility.

The species is perhaps most closely allied to *Mycomicrothelia captiosa* (p. 73) which differs in having larger and taller ascomata and a less well-developed basal fringe, and also in being lichenized and occurring on different hosts in climatically diverse areas. *M. confusa* can also occur on *Fraxinus* in Europe (p. 76), but that species has more attenuated ends to the ascospores, almost no basal fringe to the smaller ascomata, a whitish endophloeodal thallus, and always lacks an associated anamorph.

Specimen: **U.S.A.:** Massachusetts, New Bedford, 'in Fraxino', 1876, *H. Willey* (G—holotype).

II. PERIDIOTHELIA D. Hawksw., gen. nov.

Ascomata singularia, plusminusve superficialia ubi maturitata, atrobrunnea ad nigra, dimidiata, applanata sed mammiformascentia, ostiolata, non-papillata; peridium compositum e cellulis rubro-brunneis pseudoparenchymaticis subglobosis ad polyedricis; centrum cum iodo coerulescens. Hamathecium e pseudoparaphysibus compositum. Asci bitunicati, elongato-clavati ad subcylindrices, 8-spori. Ascosporae distichae, ellipsoideae, brunneae, verruculosae, 1-septatae. Anamorphosum ignotum.

Ascomata arising singly, immersed at first but soon becoming erumpent and ± superficial at maturity, dark brown to black, dimidiate at first, ± mammiform at maturity, ostiolate, ostiole depressed (not papilliform); involucrellum absent; peridium composed entirely of fungal tissue, not involving host cells as an integral part of it (not clypeate), comprising small and irregularly thickened rounded pseudoparenchymatous cells (textura globulosa) but the cells sometimes polyhedral in the angles of the ascomata and near the base (textura angularis), dark reddish brown except below the generative locule where the wall is poorly developed or almost absent at maturity, colour not changed significantly in potassium hydroxide; centrum turning blue in iodine. *Hamathecium* consisting of pseudoparaphyses; pseudoparaphyses persistent, cellular, filamentous, branched and anastomosing. *Asci* arising from the base of the ascomatal cavity, elongate clavate to subcylindrical, short-stalked, bitunicate, with an internal apical beak, discharge fissitunicate, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, rounded at the apices, 1-septate, the cells usually ± equal in size, mainly reddish brown, weakly verruculose, with a thin gelatinous sheath scarcely swelling in potassium hydroxide.

Anamorph: Unknown.

Type species: Peridiothelia fuliguncta (Norman) D. Hawksw. (holotypus).

Number of species: Three are accepted here, distinguished primarily in the size of the ascospores, but it is likely that others remain to be recognized.

Hosts: On bark, usually of living trees. Not lichenized and probably saprophytic, but sometimes appearing to have a thallus by growing through other lichenized species.

Distribution: Europe.

Observations: The generic name (*peridium* – wall; ϑηλή, *thele* – wart of nipple) recalls the nature of the ascomatal wall which distinguishes the genus from both *Kirschsteiniothelia* and *Mycomicrothelia*. I have retained the suffix '*-thelia*' for the three new generic names it has proved necessary to introduce for the main groups formerly referred to *Microthelia* to indicate a connection with both that name and *Mycomicrothelia*, i.e. *Kirschsteiniothelia, Lichenothelia*, and *Peridiothelia*.

The genus *Peridiothelia* can be referred to the family Phaeosphaeriaceae Barr (see p. 50).

Peridiothelia species are most likely to be confused with those of *Kirschsteiniothelia* and the separation of these genera is discussed on p. 50, and indicated in Table 1 and in the key to the genera (pp. 50–52).

Key to the species

1 Ascospores mainly less than 25 μm in length 2

– Ascospores (22–)25–33(–35) × (9–)10–12(–13) μm; on bark of a wide range of trees .... **2. P. grandiuscula** (p. 124)

2(1) Ascospores (16–)17–21(–24) × 7·5–9(–11) μm; on *Tilia* bark .... **1. P. fuliguncta** (p. 121)

– Ascospores (21–)22–25(–27) × 8·5–11(–11·5); on *Olea* bark .... **3. P. oleae** (p. 127)

The species

1. Peridiothelia fuliguncta (Norman) D. Hawksw., comb. nov.

Microthelia fuliguncta Norman in *Oefvers. K. VetenskAkad. Stockh.* **41** (8): 36 (1884).
Didymosphaeria fuliguncta (Norman) Vainio in *Acta Soc. Fauna Fl. fenn.* **49** (2): 151 (1921).
Tichothecium dannenbergii B. Stein ex Eitner in *Jahrb. Schles. Ges. vaterl. Cult.* **1895**: 26 (1896).
Didymosphaeria dannenbergii (B. Stein ex Eitner) Sacc., *Syll. Fung.* **17**: 683 (1905).
Polycoccum dannenbergii (B. Stein ex Eitner) Vězda in *Česká mykol.* **23**: 109 (1969).

Figs 47A–E, 48A–C.

Ascomata arising singly, scattered, colonies not delimited by a black line, erumpent, hemispherical, base applanate, 150–250(–300) μm diam, 150–180 μm tall, lacking a distinct basal fringe, ostiole somewhat depressed to slightly papillate, black; peridium dark reddish-brown, scarcely changed in potassium hydroxide, 30–50 μm thick, consisting of subglobose to polyhedral pseudoparenchymatous cells mainly 4–6 μm diam, the outer layers of cells and their interstices

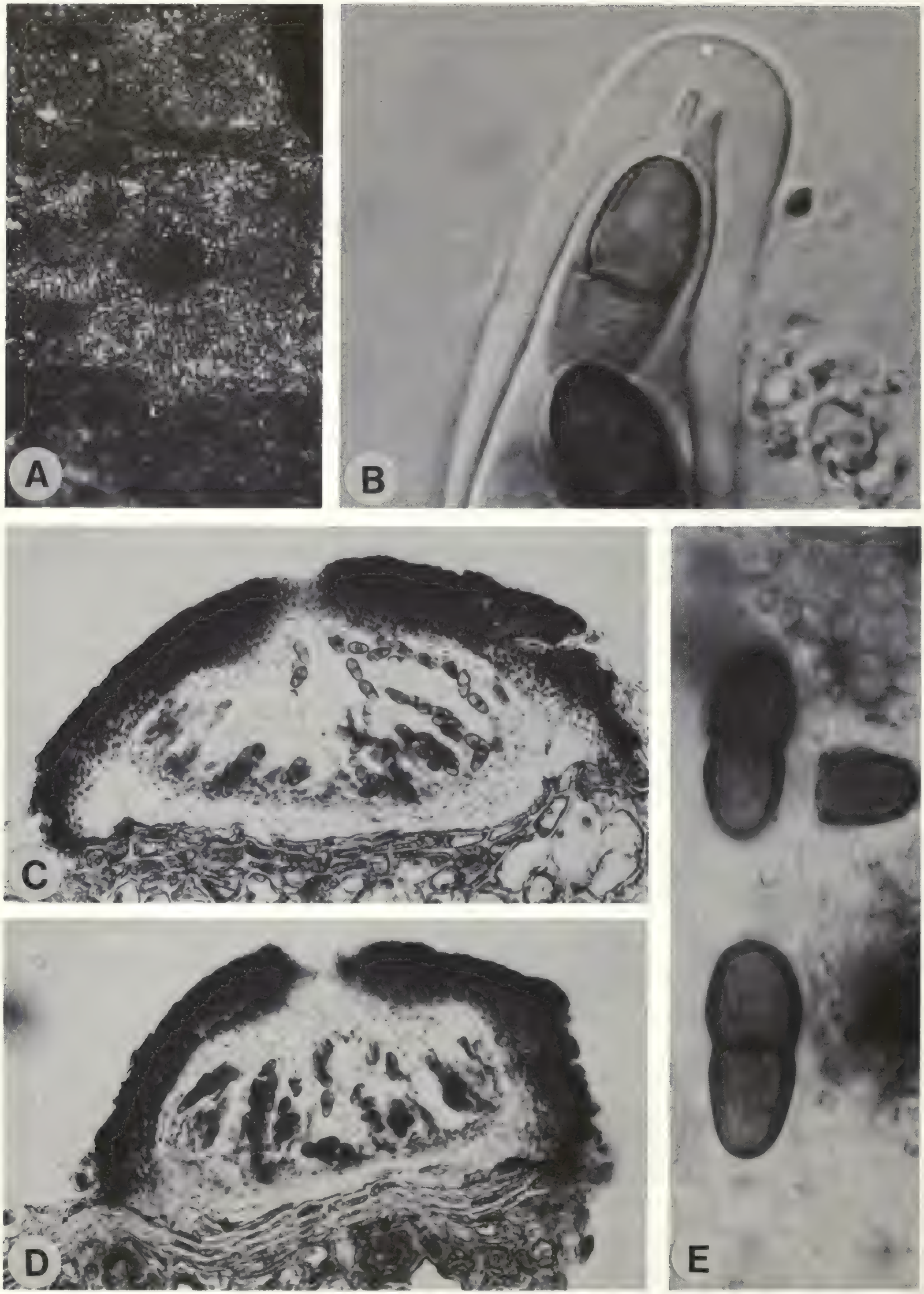

Fig. 47 *Peridiothelia fuliguncta.* **A**, Surface view (O—lectotype), × 20. **B**, Ascus apex (IMI 290531), × 2200. **C–D**, Vertical sections of ascomata (L 910.195–388), × 250. **E**, Ascospores (L 910.195-388), × 2500.

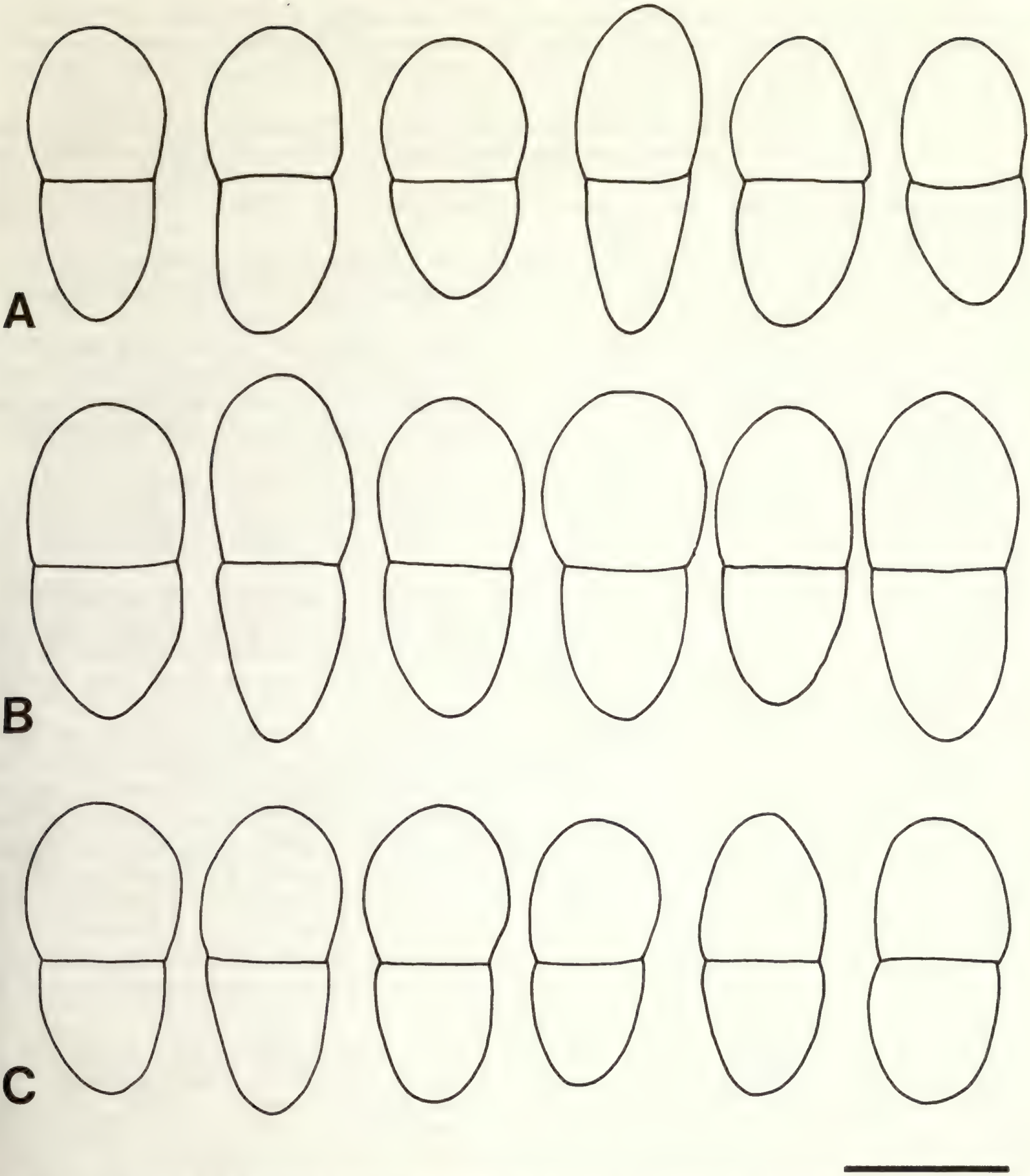

Fig. 48 *Peridiothelia fuliguncta* ascospore outlines. **A**, O—lectotype of *Microthelia fuliguncta*. **B**, WRSL—holotype of *Tichothecium dannenbergii*. **C**, L 910.195-388). Scale = 10 μm.

becoming occluded with red-brown material and sometimes difficult to differentiate in section; basal tissue almost absent at first but at maturity poorly developed, continuous or interrupted, consisting of cells similar to the peridium in all respects; ascomatal cavity lined internally by 3–7 layers of hyaline compressed pseudoparenchymatous cells; centrum turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, septate, irregularly branched and anastomosing, 2–3 μm thick. *Asci* arising from the tissue lining the base of the ascomata, ± vertically orientated, elongate-clavate to subcylindrical, short-stalked, bitunicate, with a distinct internal apical beak, 65–85 × 18–22 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, 1-septate, constricted at the septum, the cells equal in size or the lower slightly narrower, apices rounded, olive brown to reddish brown, slightly verruculose, with only a thin gelatinous sheath (to 1·5 μm thick in potassium hydroxide) scarcely apparent when mature, (16–)17–21(–24) × 7·5–9(–11) μm.

Anamorph: Unknown. Sometimes erumpent from bark with a superficial torulose dark brown mycelium which could conceivably originate from ascospores but there is no firm evidence for this.

Exsiccatae: Hepp, *Flecht. Eur.* 108 (sub *Pyrenula biformis*; K).—Schaerer, *Lich. Exs.* 109 (sub *Verrucaria biformis*; L 910.195-400).

Host: Tilia bark. Not reliably recorded from any other host. Probably never lichenized.

Distribution: Probably widespread in Europe. I have seen material from Germany, Norway, Spain, and Switzerland.

Observations: An examination of Körber's material in L (see p. 157) established unequivocably that this was the species for which Körber used the name *Microthelia micula*, a name which cannot be taken up for this species as it is illegitimate (see p. 157). Even if the name *M. micula* were legitimate, it has been used in such different senses that a case could be made for its rejection under the provisions of Art. 69.

Keissler (1936: 29) considered Norman's name to be a synonym of *Microthelia rhypontoides* (Nyl.) Keissler (in any case a later name at species rank!) but Nylander's name proves to be of uncertain application (see p. 161). Black mycelia of other fungi present on the surface of the bark may have led Keissler to this interpretation.

There are four Norman specimens labelled as *Microthelia fuliguncta* in O, and additional material in M and TRH; all have identical locality information and, although undated, undoubtedly represent syntypes. That selected here as lectotype in O has many ascomata and notes and a spore drawing by Norman; most of the other specimens have few or no mature ascomata.

The name *Tichothecium dannenbergii* was originally described as lichenicolous and has been incorrectly used for a lichenicolous species on *Pertusaria* (Vězda, 1969: 109; Hawksworth, 1975: 197). Sections of the holotype leave no doubt that that fungus arises from *Tilia* wood and merely forces its way through an overlying thallus of *P. flavida* (DC.) Laundon. The ascomata have a structure typical for *Peridiothelia* with a flattened base, the hymenial gelatin turns blue in iodine, and the ascospores are 17·5–22 × 8·5–11 μm. The lichenicolous fungus wrongly called *Tichothecium dannenbergii* has similarly sized spores but in it the hymenial gelatin does not turn blue in iodine, the ascomata are subglobose (without a flattened base), and the spores have the septum develop late and close to the base of the cell; further study suggests that this taxon is almost certainly a one-septate variant of *Adelococcus groedensis* (Zopf) Keissler.

Specimens: sine loc. (L 910.195-389). – **Germany:** Baden, 'Carlsruher Schlossgarten', on *Tilia*, 1858, *G. W. L. Körber* (L 910.195-398,-399); Nymphenberg, on *Tilia*, May 1854, *F. Arnold* (L 910.195-388); Rhön, alten Linden auf den Poppen . . . [illegible], 21 June 1880, *G. Dannenberg* (WRSL—holotype of *Tichothecium dannenbergii*; TNS—isotype). – **Norway:** Holmstrand, Järnbanegarten, on *Tilia, J. M. Norman* (O—lectotype; O, TRH, four isotypes for *Microthelia fuliguncta*). – **Spain:** Pais Vasco, Guipuzcoa, Itsasondo, on *Tilia platyphyllos*, 25 March 1984, *B. Aguirre* (IMI 290531). – **Switzerland:** see Exsiccatae.

2. **Peridiothelia grandiuscula** (Anzi) D. Hawksw., **comb. nov.**

Microthelia grandiuscula Anzi in *Comm. Soc. crittogam. Ital.* **1**: 163 (1862).
Didymosphaeria grandiuscula (Anzi) Sacc., *Syll. Fung.* **1**: 716 (1882).
Microthelia micula f. *grandiuscula* (Anzi) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1(2): 30 (1936).
Verrucaria cinerella var. *megaspora* Nyl. in *Flora, Jena* **51**: 348 (1868).
Microthelia cinerella f. *megaspora* (Nyl.) Arnold in *Flora, Jena* **53**: 485 (1870).
Microthelia micula var. *megaspora* (Nyl.) B. de Lesd. in *Bull. Soc. bot. Fr.* **53**: 688 (1907).
Microthelia micula f. *megaspora* (Nyl.) Eitner in *Jber. schles. Ges. vaterl. Kult.* I, **88**: 55 (1911).
Verrucaria micula var. *megaspora* (Nyl.) Samp. in *Broteria* (Bot.) **15**: 144 (1917).

Microthelia cinerella subvar. *megaspora* (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).

Microthelia micula f. *macrospora* Zahlbr., *Cat. Lich. Univ.* **1**: 263 (1921), nom. inval. (Art. 34.1)*

Figs 49A–D, 50A–B, 51A–C.

Ascomata arising singly, scattered, not or poorly delimited, sometimes appearing to have a thallus due to growth through overlying thalli; erumpent, to ⅔ exposed with irregularly ruptured host tissue around the base of the ascomata, broadly conical to hemispherical, applanate (150–)200–300(–325) μm diam, (80–)100–150(–170) μm tall, lacking a basal fringe, ostiole ± plane to depressed at maturity, black and shining; peridium dark reddish-brown, scarcely changed in potassium hydroxide, (15–)20–30(–35) μm thick, consisting of polyhedral thick-walled pseudoparenchymatous cells mainly 4–7 μm diam, the cells often becoming compressed radially in the outer layers, the interstices becoming occluded with red-brown material; basal tissue present from early ontogenetic stages, ± continuous but sometimes becoming interrupted in older ascomata, comprising a layer of cells to *c.* 20 μm thick in parts, cells identical to those of the upper walls; ascomatal cavity lined by hyaline strongly compressed pseudoparenchymatous to almost hyphal cells forming a layer to 15 μm thick at the base (overlying the darker-celled basal layer); centrum turning blue in iodine, at least in parts. *Pseudoparaphyses* cellular, persistent, septate, irregularly branched and anastomosing, 1·5–2·5 μm thick. *Asci* arising from the tissue lining the base of the ascomatal cavity, ± vertically orientated, elongate-clavate to subcylindrical, short-stalked, bitunicate, with a distinct long internal apical beak, short-stalked, 80–100 × 20–25 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid, 1-septate, constricted at the septum, the cells usually ± equal in size, the lower sometimes slightly narrower, apices rounded, golden-brown to reddish-brown, slightly verruculose, with a thin gelatinous sheath (to 1·5 μm thick in potassium hydroxide), (22–)25–33(–35) × (9–)10–12(–13) μm.

Anamorph: Unknown.

Exsiccatae: Anzi, *Lich. rar. Etr.* 52 (sub *Microthelia grandiuscula*; BM, K, M—isotypes of *M. grandiuscula*).

Hosts: On bark of a wide range of trees. Apparently not lichenized, but sometimes erumpent through crustose lichen thalli and then appearing from above to have a thallus of its own.

Distribution: Probably widespread in continental Europe. I have seen material from France, Italy, and Norway, but there are also reports (as var. *megaspora*) at least from Germany (Grummann, 1963), Poland (Nowak &Tobolewski, 1975), and the U.S.S.R. (Kopaczevskaja et al., 1977).

Observations: This fungus is readily separated from *Peridiothelia fuliguncta* by the longer and broader ascospores; it also appears to be much less restrictive in its host range.

Care is sometimes needed to distinguish this species from *Kirschsteiniothelia aethiops* which has ascospores of an almost identical size, (21–)25–33(–38) × (7·5–)8·5–12(–14) μm (Hawksworth, 1985*a*), but tending to be more strongly attenuated rather than rounded at the apices as is usual in *P. grandiuscula*. The ascomata also differ in their structure and the palisade-like arrangement of cells in the angles of the ascomatal cavity are not seen in *P. grandiuscula*. In addition, the centrum of *K. aethiops* is typically I−, the ascomata normally occur directly on decaying lignum and are only rarely erumpent through the bark of living trees, and the conidiophores of the *Dendryphiopsis* anamorph of *K. aethiops* are often to be found in association with its ascomata. *K. aethiops* also has a much wider distribution in temperate regions, occurring in North America and Australasia as well as in Europe.

In the original publication of the epithet *'megaspora'*, Nylander gave the collection details as 'Ad cortices in Gallia (*Crouan, Ripart*) et in Anglia (*Crombie*)'. In H there are specimens from all of these collectors, but those of the Crouan brothers (Brest, H-NYL 686) and Crombie (New Forest, H-NYL 692; also a later one from the same site, 1869, H-NYL 690 and an undated one in BM [all on *Fagus*]) are of a *Massarina* Sacc. species with spores becoming pale brown at a late stage of development and also 3-septate and to 38·5 × 10·5 μm. That of Ripart, however, is a

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* Zahlbruckner (loc. cit.) attributed this name to Eitner (loc. cit.), but inspection of that work showed Eitner to have used 'f. *megaspora* Nyl.'; *'macrospora'* was thus a 'lapsus' by Zahlbruckner.

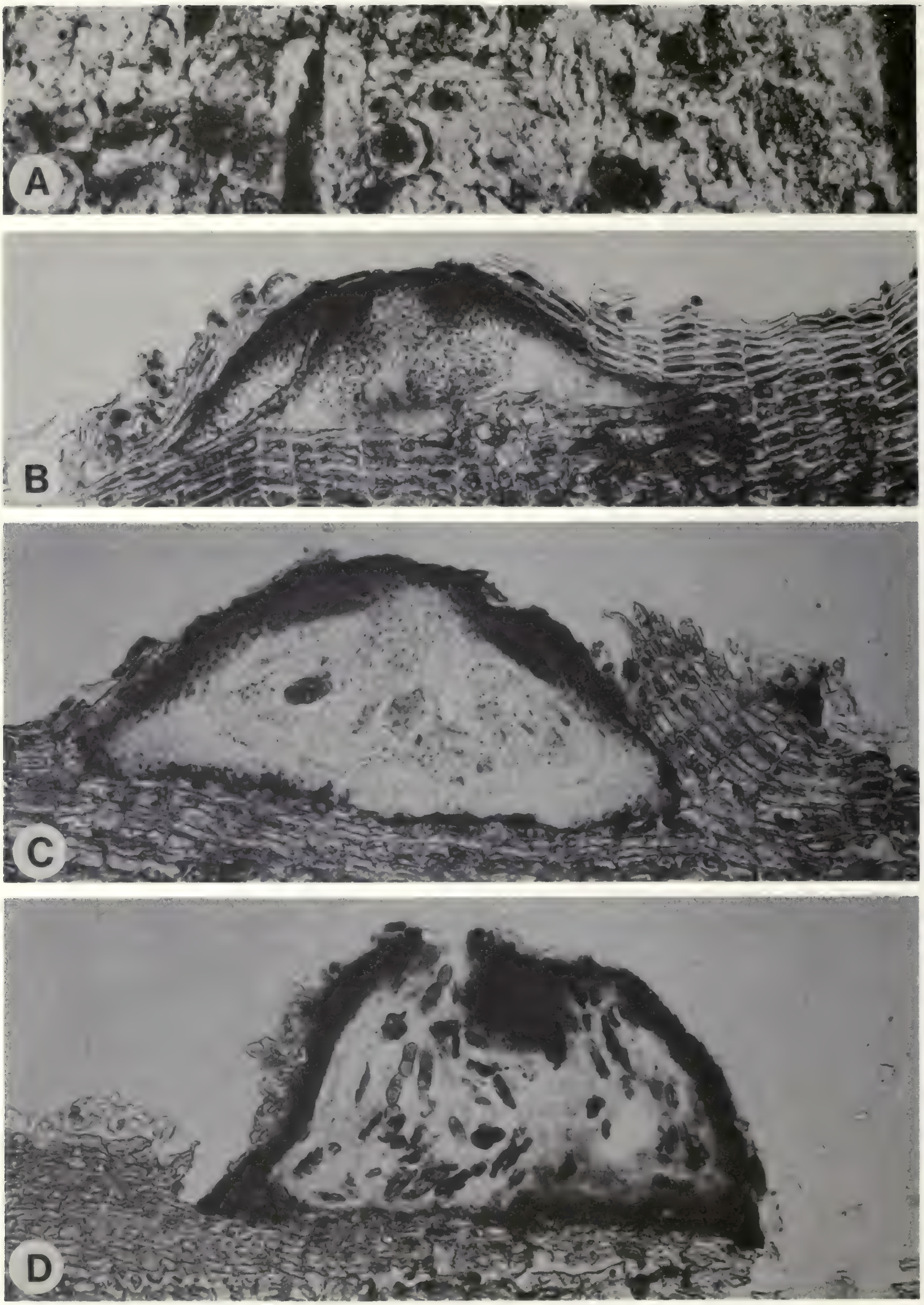

Fig. 49 *Peridiothelia grandiuscula* (BM—isotype). **A**, Surface view, × 20. **B–D**, Vertical sections of ascomata in increasing stages of maturation, × 250.

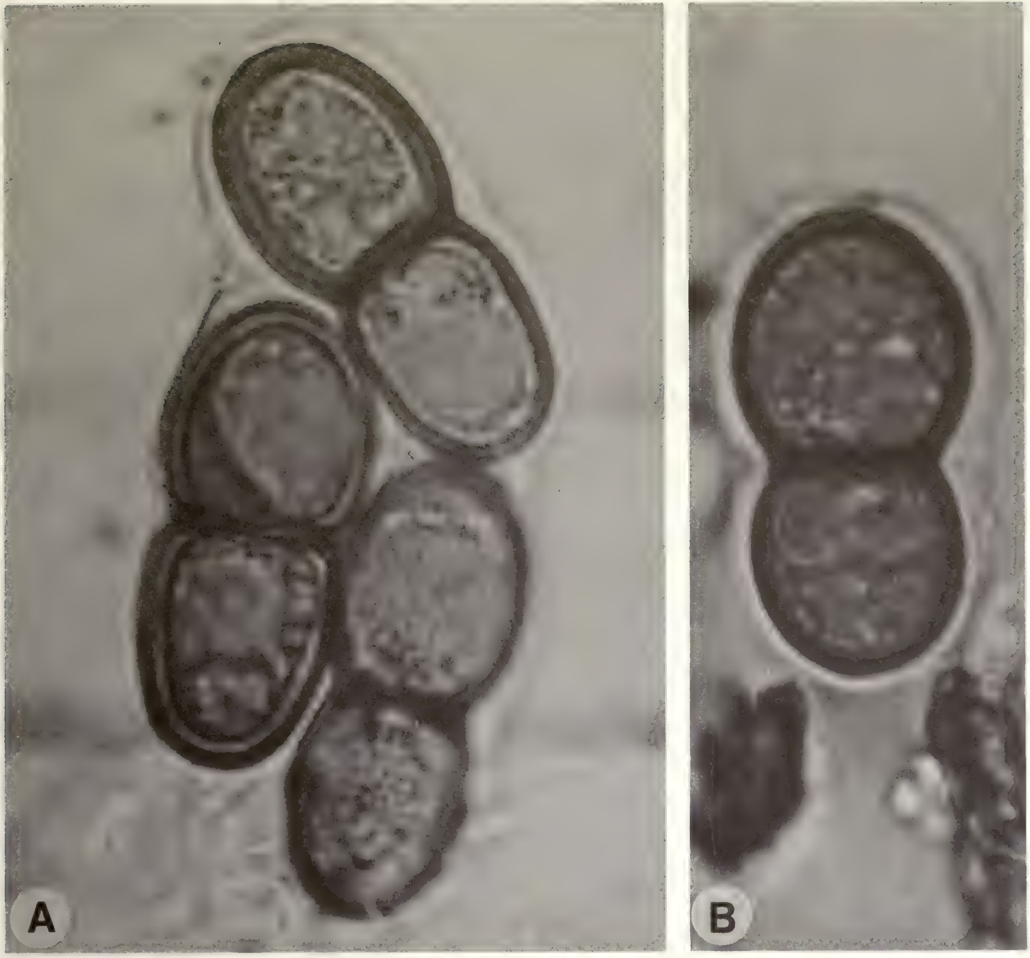

Fig. 50 *Peridiothelia grandiuscula* (M—isotype). **A**, Group of ascospores still enclosed in the ascus, × 2500. **B**, Released ascospore, × 2500.

Peridiothelia identical to *grandiuscula* and, to accord with subsequent use of the name, Ripart's collection is selected here as the lectotype for Nylander's epithet.

Microthelia membranacea Anzi may be an additional synonym of this species but type material has not been located (see p. 156).

Specimens: **France:** Marronnier, Chavanner, 26 March 1867, *J. Ripart* 1027b (H-NYL 697—lectotype of *Verrucaria cinerella* var. *megaspora*). – **Italy:** 'Ad arborum truncos supra Florentiam (Parco di Pratolino)', *M. Anzi* [*Lich. rar. Etr.* exs. 52] (BM, K, M—isotypes of *Microthalia grandiuscula*). – **Norway:** Troms, Bardu Sefermoen, on *Alnus incana* bark, August 1976, *D. O. Øvstedal* (BG).

3. **Peridiothelia oleae** (Körber) D. Hawksw., **comb. nov.**

Microthelia oleae Körber in *Verh. zool.-bot. Ges. Wien* **17**: 706 (1867).

Fig. 52A–C.

Ascomata arising singly, scattered, colonies not delimited by a black line, erumpent, hemispherical, applanate, 200–300 μm diam, 150–220 μm tall, lacking a distinct basal fringe, ostiole plane to slightly papillate, black; peridium dark reddish brown, scarcely changed in potassium hydroxide, 25–45 μm thick, consisting of subglobose to polyhedral pseudoparenchymatous cells mainly 6–9 μm diam but becoming almost hyphal near the ostiolar canal; basal tissue poorly

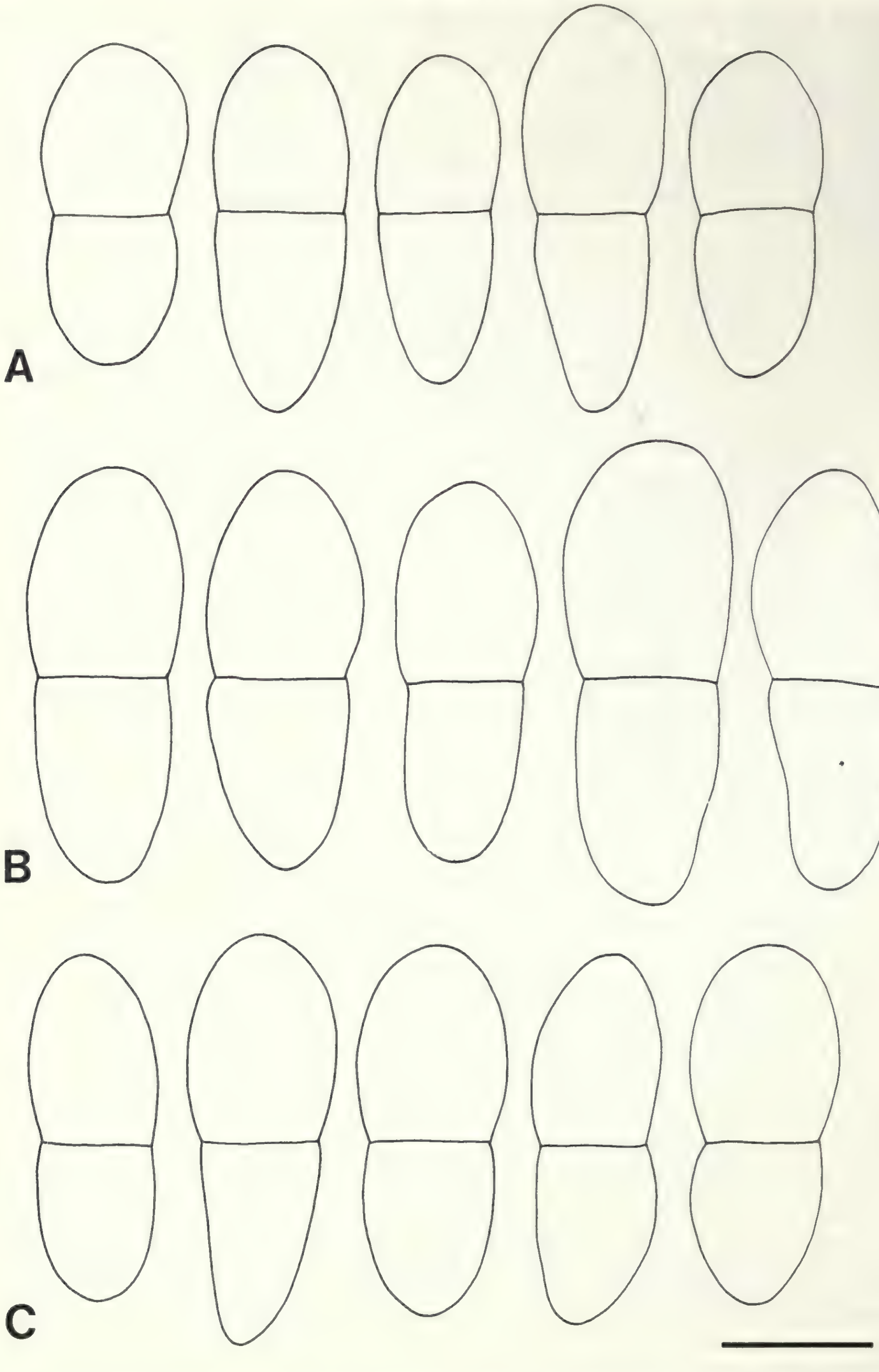

Fig. 51 *Peridiothelia grandiuscula* ascospore outlines. **A**, K—isotype of *Microthelia grandiuscula*. **B**, H-NYL 697—lectotype of *Verrucaria cinerella* var. *megaspora*. **C**, *Øvstedal*, BG. Scale = 10 μm.

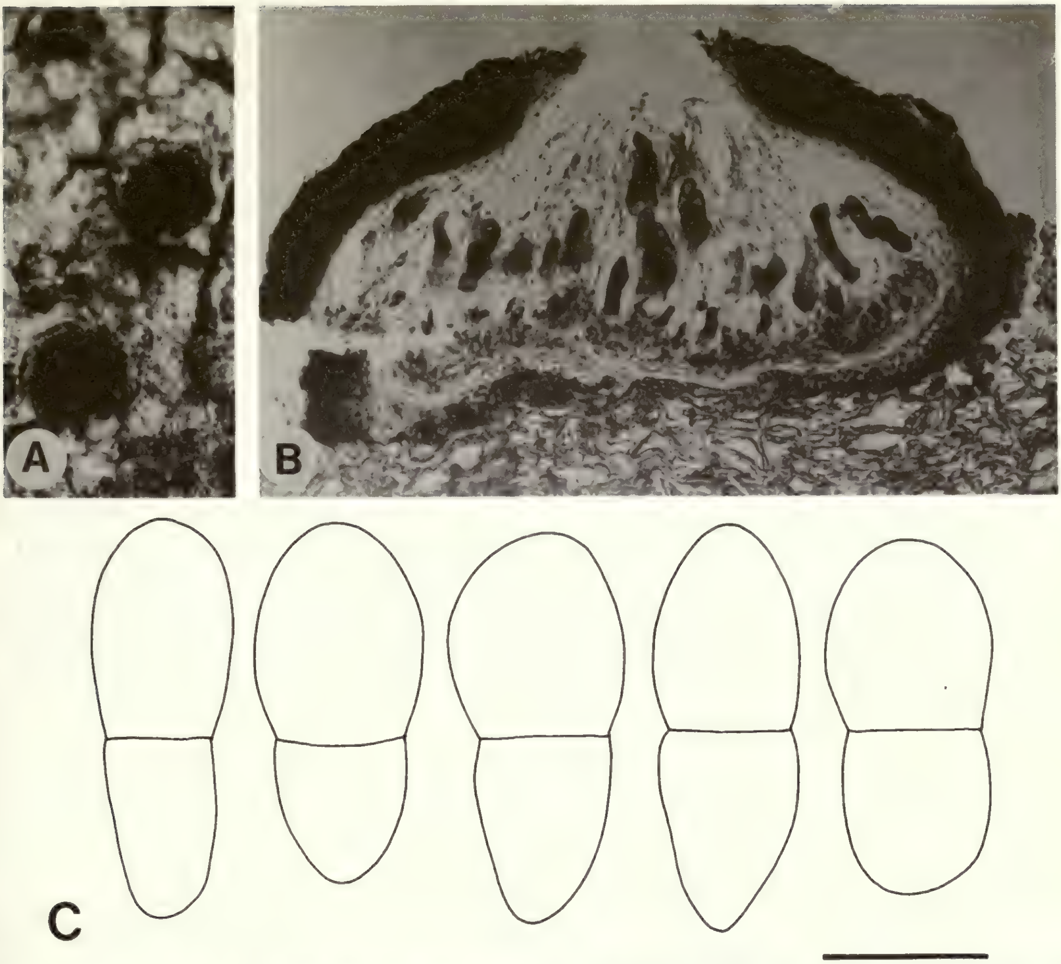

Fig. 52 *Peridiothelia oleae* (L 910.195-407—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

developed, continuous or interrupted, consisting of cells similar to those of the peridium but mainly 7–10 μm diam; ascomatal cavity lined internally by 3–5 layers of hyaline strongly radially compressed pseudoparenchymatous cells but becoming hyphal with the formation of pseudoparaphyses; centrum turning blue in iodine. *Pseudoparaphyses* cellular, persistent, numerous, septate, branched and anastomosing, 1·5–2·5 μm thick. *Asci* arising from the base of the ascomata, ± vertically orientated, elongate-clavate to subcylindrical, without a distinct stalk, bitunicate, with an internal apical beak, 75–90 × 20–25 μm, 8-spored. *Ascospores* distichously arranged in the asci, ellipsoid to soleiform, 1-septate, constricted at the septum, the lower cell somewhat shorter, apices usually rounded but that of the lower cell sometimes attenuated, golden brown, slightly verruculose, with a distinct gelatinous sheath (to 2·5 μm thick in potassium hydroxide), (21–)22–25(–27) × 8·5–11(–11·5) μm.

Anamorph: Unknown.

Host: Olea europaea bark. Reports from *Ficus carica* and *Quercus ilex* (Kusǎn, 1953) are probably based on misdeterminations.

Distribution: Yugoslavia. Known only from the original collection.

Observations: This little known species should not be confused with *Mycomicrothelia inaequalis* (see p. 90) which occurs on decorticate *Olea* at least in France. In addition to the differences in structure of the ascomata, the centrum in that species does not react with iodine and the ascospores are distinctly smaller, more unequally celled, and almost smooth.

At first I thought that the recently described *Massariella oleae* M. Corte (Montemartini Corte, 1983) might be a later synonym of *Peridiothelia oleae*. This fungus causes distinctive bark cankers on olives in Italy. However, examination of an isotype kindly sent to me by Professor Montemartini Corte (Liguria, Chiavari, June 1978, *A. Montemartini Corte*, IMI 291258) showed the ascomata to be completely immersed, to 900 μm wide, with thick-walled ascospores 22–33 × 18–11 μm borne uniseriately in the asci.

Specimens: **Yugoslavia:** Dalmatia, Megline, on *Olea europaea* bark, *F. W. Weis* (L 910.195-407—holotype of *Microthelia oleae*; M—isotype).

Excluded species

This section considers the identities of 143 taxa either described in, transferred to, or mentioned as synonyms of *Microthelia*, or other generic names considered in this revision (i.e. *Anzia, Kirschsteiniella, Mycomicrothelia*) which are not treated in the preceding sections. Those referred only to *Astrosphaeriella* (or its synonyms) are, however, excluded, as they have been discussed elsewhere (Hawksworth, 1981*a*). Names are arranged in alphabetical order by their epithets, whether specific or infraspecific.

Microthelia acerina Rossman & Wilcox in *Mycologia* **77**: 162 (1985).

Type: U.S.A., New York, Onondaga County, Syracuse, in Oak Wood Cemetery, on absorbing mycorrhizal rootlets of *Acer saccharum*, 26 October 1983, *H. E. Wilcox* (BPI—holotype non vidi).

I have studied an authentic collection of this species from the type locality (7 November 1979, *H. E. Wilcox*, IMI 245174) and find that it represents a species of *Kirschsteiniothelia*. See Hawksworth (1985*a*).

Microthelia adspersa Körber ex B. Stein *in* Cohn, *Krypt.-Fl. Schles.* **2** (2): 332 (1879).

Type: Poland, near Hirschbergam, 'in sylva "Sattler"', on *Populus tremula, G. W. Körber* [*Lich. sel. Germ.* exs. 326] (M—2 isotypes).

Microthelia adspersa Körber, *Lich. sel. Germ.* exs. 326 (1868), nom. inval. (Art. 32.1).

As reported by Keissler (1937: 256), Körber's material is *Leptorhaphis atomaria* (Ach.) Szat. (syn. *L. tremulae* var. *lucida* (Körber) Keissler), a species with falcate hyaline 1–3 septate ascospores 16–30 × 3–4 μm. Stein, however, described a different fungus with multi-spored asci and brown ascospores 7–10 × 2–3 μm which scarcely became divided; his description is certainly that of a *Muellerella* species, probably *M. lichenicola* (Sommerf. ex Fr.) D. Hawksw. according to the width of the spores and assuming some were truly 1-septate when fully mature. As Stein did not intend to describe a new species but applied Körber's name, the epithet should be typified by Körber's exsiccate and placed as an additional synonym of *L. atomaria* (see p. 135).

Microthelia thelena var. **albicans** Müll. Arg. in *Bot. Jb.* **6**: 417 (1885).

Type: Cuba, *sine loc., C. Wright* [Verr. Cub. II exs. 648] (G—holotype).

Fig. 53A–C.

This taxon produces pseudostromatic dimidiate ascomata (450–)500–700(–800) μm diam with trabeculate branching and rarely septate pseudoparaphyses 1–1·5 μm thick. The ascospores seen by me were 29·5–34 × 9–11 μm and thick-walled, mainly 1–3 septate but developing up to five septa in some cases. The inner walls are thickened in the way characteristic of *Pyrenula* s. lat., although the dimidiate ascomata and slightly verruculose ascospores are atypical for that genus. Pending a revision of the tropical Pyrenulaceae this taxon is best referred to *Pyrenula* s. lat.

Verrucaria thelena var. **albidior** Nyl. in *Annls Sci. nat., Bot.* IV, **20**: 254 (1863).

Type: Nicaragua, comm. E. Tuckerman 'Verr. 22' (H-NYL 714—lectotype).

Microthelia thelena var. *albidior* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **1**: 266 (1921).

Fig. 54A–C.

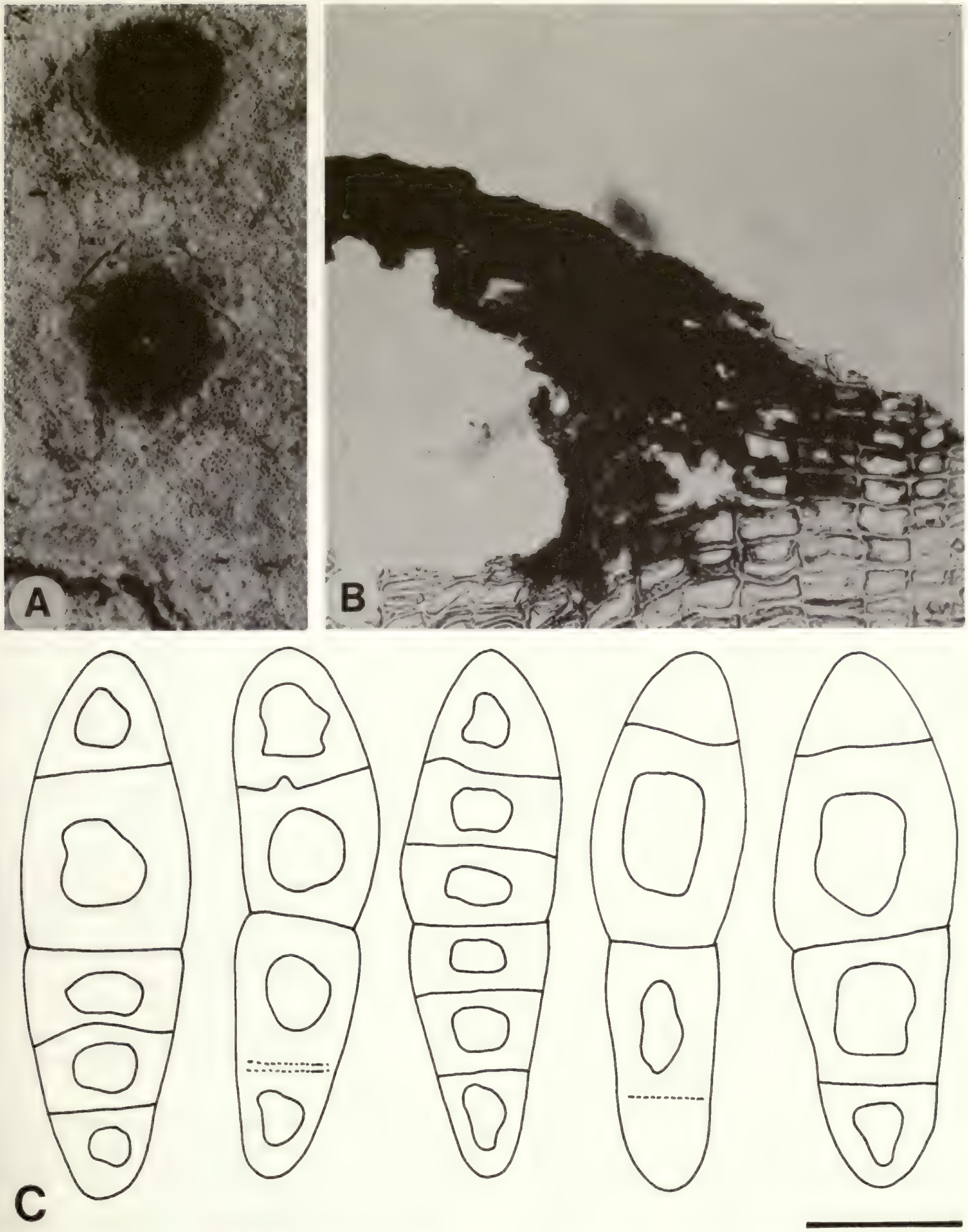

Fig. 53 *Microthelia thelena* var. *albicans* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma margin, × 250. **C**, Ascospore outlines, scale = 10 μm.

Two specimens were mentioned when this variety was first described: that from Nicaragua, selected as lectotype above, and one from Hong Kong (comm. Tuckerman 'Verr. 21', H-NYL 715). These two specimens are not congeneric and that from Nicaragua is chosen as the lectotype as it was the first mentioned. The lectotype has a *Mycomicrothelia*-like structure in vertical section, but the pseudoparaphyses are trabeculate and the ascospores (14–16 × 7–8 μm) remain hyaline for a long time, only very old

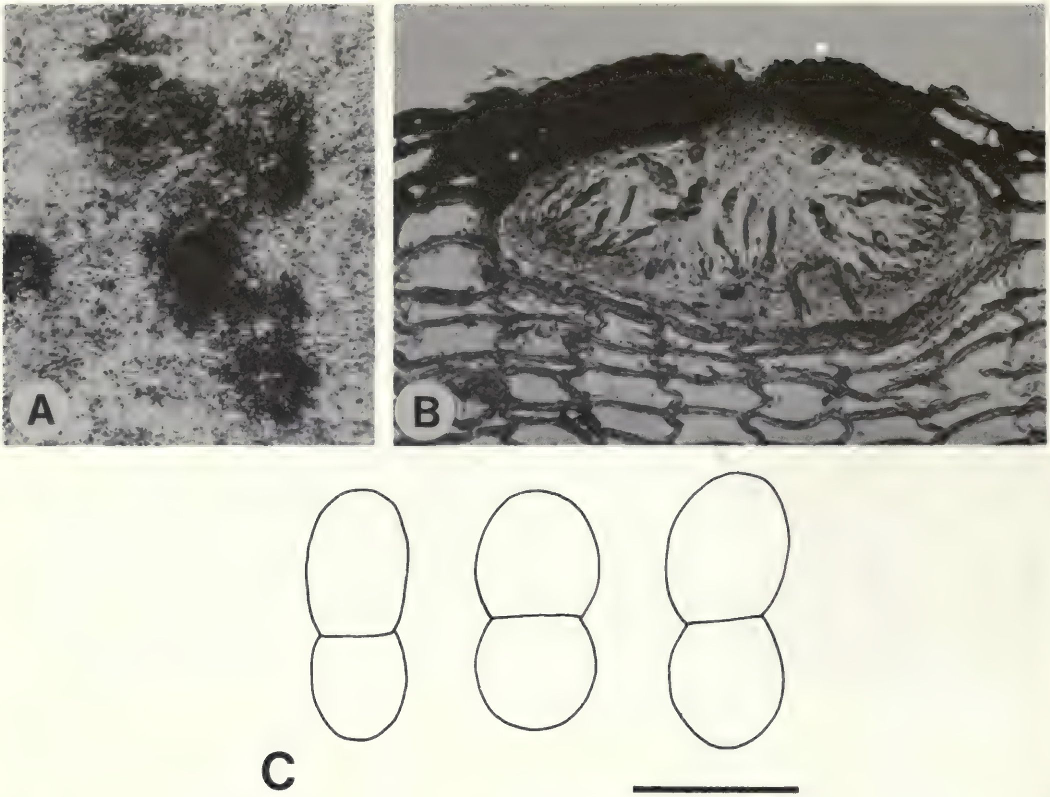

Fig. 54 *Verrucaria thelena* var. *albidior* (H-NYL 714—lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma. × 250. **C**, Ascospore outlines, scale = 10 μm.

spores becoming slightly brownish-tinged and verruculose; this collection can therefore be referred to *Anisomeridium* (Müll. Arg.) M. Choisy, a decision supported by the rather swollen cells of the ascospores and the smaller basal cell. In the collection from Hong Kong the pseudoparaphyses are again trabeculate and the ascospores of a similar size, but these are brown from a very early stage, have a central septum, and remain smooth-walled when studied at the highest magnification of light microscopy; the position of this collection is uncertain.

Verrucaria epidermidis var. **albissima** Ach. in *K. svensk VetenskAkad. Handl.* **30**: 149 (1809).

Type: Sweden, on *Betula* bark (BM-ACH 282(3)—? isotype).

For obligate synonyms see Zahlbruckner (1921–22: 265, 341–342) who listed this epithet both as a doubtful synonym of the fungus now known as *Leptorhaphis epidermidis* (Ach.) Th. Fr. and of *Microthelia sexlocularis* Müll. Arg.; the latter name was introduced for the taxon to which Fée (1824) misapplied Acharius' name (see p. 165).

Vainio (1921*b*: 188) reported that the material in H-ACH was a coelomycete with hyaline, arcuate conidia 20–22 × 2–3 μm. According to an annotation label by Dr R. C. Harris on the Acharian specimen in BM, that also consists of an unidentified coelomycete forming non-septate acicular conidia; this consequently appears to be identical to the taxon in Helsinki.

Microthelia alcicornaria Lindsay in *Q. Jl Microsc. Sci.* II, **9**: 349 (1869).

This taxon was lectotypified by Hawksworth (1981*c*) who found it to be an earlier name for the lichenicolous coelomycete previously called *Lichenosticta podetiicola* Zopf. The combination *L. alcicornaria* (Lindsay) D. Hawksw. was published in Hawksworth *et al.* (1980) and a full synonymy, description, and illustrations are included in Hawksworth (1981*c*).

Didymosphaeria alpina Hazslin in *Verh. zool.-bot. Ges. Wien* **23**: 365 (1873).

Amphisphaeria alpina (Hazslin) Hazslin in *Math. Termés. Közlem.* **25**: 65 (1892).
Amphisphaeria pinicola Sacc., *Syll. Fung.* **1**: 726 (1882), as 'Rehm', nom. illegit. (Art. 63.1).
Astrosphaeriella pinicola (Sacc.) Scheinpflug in *Ber. schweiz. bot. Ges.* **68**: 372 (1958).
Non *Amphisphaeria betulina* f. *pinicola* Rehm, *Ascom.* exs. 135 (1872), nom. inval. (Art. 32.1).

Hazslin (loc. cit.) described this species from *Pinus* bark in 'Alpe Retyerát in Siebenbürgen', now part of Romania. He indicated that it formed adnate hemispherical ascomata with a raised ostiole and producing linear asci with monostichous, oval, 1-septate, dark fuscous ascospores 25 × 7 μm. The name was also published elsewhere by Hazslin in the same year according to Saccardo (1882: 726), who gives the bibliographical citation as 'Hözlem. Banat. 1873, p. 49 fig. 16'. This refers to *Math. Termés Közlem.* **10**: 49, the title-page of which is dated '1875', but the volume could have been issued in parts. This paper includes an illustration (tab. 14 fig. 16 *a–c*) showing in addition to the above features broad, unbranched, filiform paraphyses.

Rehm's fungus belongs to *Kirschsteiniothelia aethiops* (see Hawksworth, 1985*a*) but when the epithet was first validly published by Saccardo (loc. cit.) Hazslin's name was cited as a synonym. As pointed out by Hawksworth (1981*a*) the name is then superfluous and illegitimate and further automatically typified by the type of Hazslin's name which should have been adopted under the Code (Art. 7.11).

No type or authentic material of Hazslin's fungus has been located by any recent workers and was not found by me in BP. As the ascospores were said to be (a) monostichously arranged, (b) only 7 μm wide, and (c) simple paraphyses were illustrated, I consider that it would be most unwise to take up '*alpina*' as the correct name for the species treated as *K. aethiops* until indisputable evidence as to its identity becomes available. A placement in *Amphisphaeria* seems likely to be correct.

Verrucaria ambulatrix Nyl. in *Flora, Jena* **64**: 182 (1881).

Microthelia ambulatrix (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).
Arthopyrenia ambulatrix (Nyl.) Zahlbr., *Cat. Lich. Univ.* **1**: 269 (1921).

This species was described as lacking paraphyses and producing 3-septate ascospores 11–12 × 4·5 μm. Keissler (1936: 48) consequently regarded it as a synonym of *Phaeospora parasitica* (Lönnr.) Arnold.

Microthelia ambigua Zahlbr. in *Reprium Spec. nov. Regni veg.* **31**: 199 (1933).

Type: Taiwan ['Formosa'], on bark, *Y. Asahina* F314 (W 1931/691—holotype).

The ascospores in this species prove to be hyaline when discharged from the asci, broadly fusiform, 1(–3)-septate, strongly constricted at the central septum (and sometimes breaking into part-spores), smooth to slightly granular, with a gelatinous sheath, and measure (20–)23–26(–28) × 7–8 μm. Some ascospores, which are senescent because they are not discharged but retained in the asci beyond maturity, develop a pale brownish colour and have walls which appear to be somewhat ornamented. It was the presence of old brownish spores which led to Zahlbruckner's placing of the species in *Microthelia*, but such spores are a common feature of many species of *Arthopyrenia* Massal. s. str. (Harris, 1975), to which genus this species is most appropriately referred. The occasional occurrence of part-spores is suggestive of *Sporoschizon* Riedl, a genus whose relationship with *Arthopyrenia* s. str. is in need of re-investigation.

Lichen analeptus Ach., *Lich. Suec. Prodr.*: 15 (1798).

For obligate synonyms see Zahlbruckner (1921: 269–271).

Vainio (1921*b*: 209) reported that material under this name in H-ACH was a mixture of *Arthopyrenia punctiformis* Massal. and '*Microthelia micula*'. However, when Acharius introduced this epithet he cited *Verrucarria olivacea* Pers. as a synonym; his name is not superfluous but a new name because of the existence of the earlier *Lichen olivaceus* L. (i.e. *Parmelia olivacea* (L.) Ach.). Persoon (1794: 28) based his name on '*Lichen cinereo-fuscus* Wulfen (Jacq.-Coll. 2 tab. 14 fig. 4)' which is a misapplication of an earlier name of Jacquin's listed by Zahlbruckner (1926*b*: 421) under *Baeomyces rufus* (Huds.) Rebent. The illustration provided by Persoon is of a crustose lichen with a definite brownish-grey thallus and small dot-like black ascomata. It is most unlikely that Wulfen's or Persoon's material belonged to either of the species under this name in H-ACH and the name must be treated as of uncertain application.

As pointed out by Harris (1975: 37), this leads to considerable difficulties over the generic names *Arthopyrenia* Massal., *Arthopyreniomyces* Cif. & Tom., *Leiophloea* (Ach.) Gray, and *Pyrenillium* Clem., all of which were originally based on *Lichen analeptus*. In my opinion, *Arthopyrenia* Massal. should be proposed for conservation with *A. rhyponta* (Ach.) Massal. as the lectotype species to avoid unfortunate name changes at both the generic and specific levels.

Verrucaria analtiza Stirton in *Trans. Glasgow Soc. Fld Nat.* **4**: 95 (1876).

Type: Australia, New South Wales, Riverina, on bark, 28 September 1875, *H. Paton* (BM—isotype).

Microthelia analtiza (Stirton) Zahlbr., *Cat. Lich. Univ.* **1**: 255 (1921).

Examination of the isotype in BM established that this was an immersed pyrenomycete with brown, smooth, 1-septate, ellipsoid ascospores mainly measuring 10–11 × 4 μm, ascomata which were slightly clypeate above, with most of the wall ± hyaline, and the spores uniseriately arranged in the asci. This material falls within the range of variation of the omnivorous *Didymosphaeria futilis* (Berk. & Broome) Rehm (see Scheinpflug, 1958: 340–344). Zahlbruckner (loc. cit.) gave the locality as Tasmania but the label in BM states 'N.S. Wales'. According to Rogers (1982: 509), type material is also present in GLAM; that specimen should be treated as the holotype.

Buellia anthracina Anzi in *Atti Soc. Ital. Sci. nat.* **11**: 171 (1868), nom. illegit. (Art. 63.1).

Microthelia anthracina (Anzi) Arnold in *Verh. zool.-bot. Ges. Wien* **23**: 112 (1873), nom. illegit. (Art. 63.1).

A superfluous name for *Rinodina aterrima* Krempelh. ex Anzi; see p. 135 and Hawksworth (1981*b*).

Microthelia metzleri f. **anthracina** J. Steiner *in* Beck & Zahlbruckner in *Annln naturhist. Mus. Wien* **9**: 136 (1894).

A later synonym of *Lichenothelia scopularia* (Nyl.) D. Hawksw. (Hawksworth, 1981*b*).

Astrosphaeriella aosimensis Hino & Katumoto in *Bull. Fac. Agric. Yamaguti Univ.* **7**: 262 (1956).

Microthelia aosimensis (Hino & Katumoto) E. Müller *in* Müller & von Arx in *Beitr. Kryptog.-fl. Schweiz* **11** (2): 286 (1962).

An isotype was studied by Hawksworth (1981*a*) who found this to be a valid species of *Astrosphaeriella*.

Sphaeria applanata Fr., *Obs. mycol.* **1**: 181 (1815) : Fr., *Syst. mycol.* **2**: 463 (1823).

Microthelia applanata (Fr.) E. Müller *in* Müller & von Arx in *Beitr. Kryptog.-fl. Schweiz* **11** (2): 286 (1962).

Kirschsteiniella applanata (Fr.) Petrak in *Annls mycol.* **23**: 331 (1923).

This epithet has been incorrectly applied to the species now known as *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw. by many authors since Fuckel (1870) misused the epithet, but was found to have been employed by Fries for a species belonging to the coelomycete genus *Cyclothyrium* Petrak. See Hawksworth (1981*a*) for a list of combinations based on Fries' name.

Microthelia araucana Speg. in *Revta Fac. Agron. Vet. La Plata* II, **6**: 71 (1910).

Type: Chile, Bahía de Corral, on *Rubus sanctus* dry branches, January 1909, *C. Spegazzini* (LPS 5777—holotype).

Didymosphaeria araucana (Speg.) Sacc. & A. Trotter *in* Saccardo, *Syll. Fung.* **22**: 171 (1913).

The holotype produces immersed clypeate ascomata with excentrically inserted ostioles and cylindrical asci about 120 × 9 μm with uniseriately arranged ascospores, and trabeculate pseudoparaphyses 1–1·5 μm thick. The ascospores have a longitudinal striate ornamentation when mature and measure 15·5–21 × 7·5–9 μm. This taxon appears to fall within the range of variation of *Didymosphaeria rubicola* Berl., a fungus well-known on other *Rubus* species, and Spegazzini's name should be treated as an additional synonym of that species.

Microthelia araucariae Speer in *Bull. trimest. Soc. mycol. Fr.* **99**: 283 (1983).

Type: Brasil, Rio Grande do Sul, Cambara do Sul, on branches and trunks of *Araucaria angustifolia*, 13 March 1976, *E. O. Speer* (non vidi).

Although I have not had the opportunity to study material of this recently described species, the excellent illustrations provided by Speer (loc. cit.) show that this fungus belongs to the Melanommataceae. The narrow fusiform ascospores, given as 58–63 × 5 μm, recall those of some *Astrosphaeriella* species, but the ascoma in *M. araucariae* appears to have a quite different structure to that seen in all *Astrosphaeriella* species currently known (Hawksworth, 1981*a*; Hawksworth & Boise, 1985). The fungus merits critical study and may well prove to represent a hitherto unrecognized genus.

According to Dr J. Mouchacca (in litt.) material of this taxon has not been deposited in PC as indicated in the original account, and consequently could not be obtained on loan. Dr Speer has recently changed positions and I have not been able to contact him directly.

Verrucaria arctata Stirton in *Proc. phil. Soc. Glasg.* **11**: 320 (1879).

Type: India, on bark, *G. Watt* (BM—isotype).

Microthelia arctata (Stirton) Zahlbr., *Cat. Lich. Univ.* **1**: 255 (1921).

Fig. 55A–D.

The subglobose ascomata are completely immersed in the bark, to 700 μm diam, and with a peridium composed of brown subglobose pseudoparenchymatous cells. In vertical section a definite beak-like ostiole is seen to penetrate the upper bark layers and a whitish crustose thallus. The ascospores remain hyaline within the asci for a considerable time, but finally become brown and 3-septate when mature, with the secondary septa closer to the apices than the median septum, soleform, with rounded or attenuated apices, ± smooth-walled, with a thin gelatinous sheath, and measure 32–42(–45) × 12–15(–20) μm; the pseudoparaphyses are trabeculate and *c.* 1·5 μm wide. The fungus appears to belong to the genus *Splanchnonema* Corda, but cannot be accommodated within the species generally accepted in Europe and North America (see Barr, 1982; Shoemaker & Le Clair, 1975).

Microthelia asiatica Vainio in *Hedwigia* **46**: 180 (1907).

Type: Thailand, Gulf of Siam, Ko Chang ['Koh Chang'], 'ad corticem arboria', 1900, *J. Schmidt* [hb. Vainio 34277] (TUR 32852—holotype).

Fig. 56A–B.

The ascospores in this melanommataceous fungus are essentially hyaline and only become slightly brownish and slightly verruculose when degenerating. The hyaline ascospores are mainly about 15 × 7 μm and those with a brownish tinge are 17–20 × 7 μm. No thallus is visible and the fungus is presumably not lichenized. This species may well belong to *Anisomeridium* (Müll. Arg.) M. Choisy but no transfer is made here as the tropical species of that genus as so imperfectly understood.

The report of this taxon from Assam (Roychoudhury, 1973) may well refer to a different species, but I have not seen the material.

Rinodina aterrima Krempelh. ex Anzi in *Comm. Soc. crittog. Ital.* **2**: 11 (1864).

Microthelia aterrima (Kempelh. ex Anzi) Zahlbr., *Cat. Lich. Univ.* **1**: 255 (1921).

A later synonym of *Lichenothelia scopularia* (Nyl.) D. Hawksw. For further obligate synonyms see Hawksworth (1981*b*).

Microthelia ecatonspora var. **athallina** Müll. Arg. in *Flora, Jena* **53**: 168 (1870).

Type: Switzerland, Grand Muveran, on *Protoblastenia incrustans* (DC.) Steiner, 25 August 1869, *J. Müller-Argoviensis* (G—holotype).

This is a species of *Muellerella* very similar to *M. lichenicola* (Sommerf. ex Fr.) D. Hawksw. in the size of its ascospores (5–7·5 × 2–3·5 μm), but differs in that the ascomata are unusually large for that species, measuring 100–200 μm diam. The ascomata are, however, immersed in minute pits in the rock amongst apothecia of the *Protoblastenia*, and it is possible that this has enabled them to grow larger than is usual for the species. For the moment it seems prudent to take the latter view and treat this name as a synonym of *M. lichenicola* rather than introduce a new combination.

Lichen atomarius Ach., *Lich. Suec. Prodr.*: 16 (1798).

Verrucaria atomaria (Ach.) Mérat, *Nouv. Fl. Env. Paris*, 2nd ed., **1**: 160 (1821).
Microthelia atomaria (Ach.) Körber, *Syst. Lich. Germ.*: 373 (1855).
Didymosphaeria atomaria (Ach.) Rehm *in* Saccardo, *Syll. Fung.* **1**: 715 (1882).
Leptorhaphis atomaria (Ach.) Szat. in *Magy. bot. Lap.* **26**: 31 (1928 ['1927']).
Mycomicrothelia atomaria (Ach.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 33 (1936).

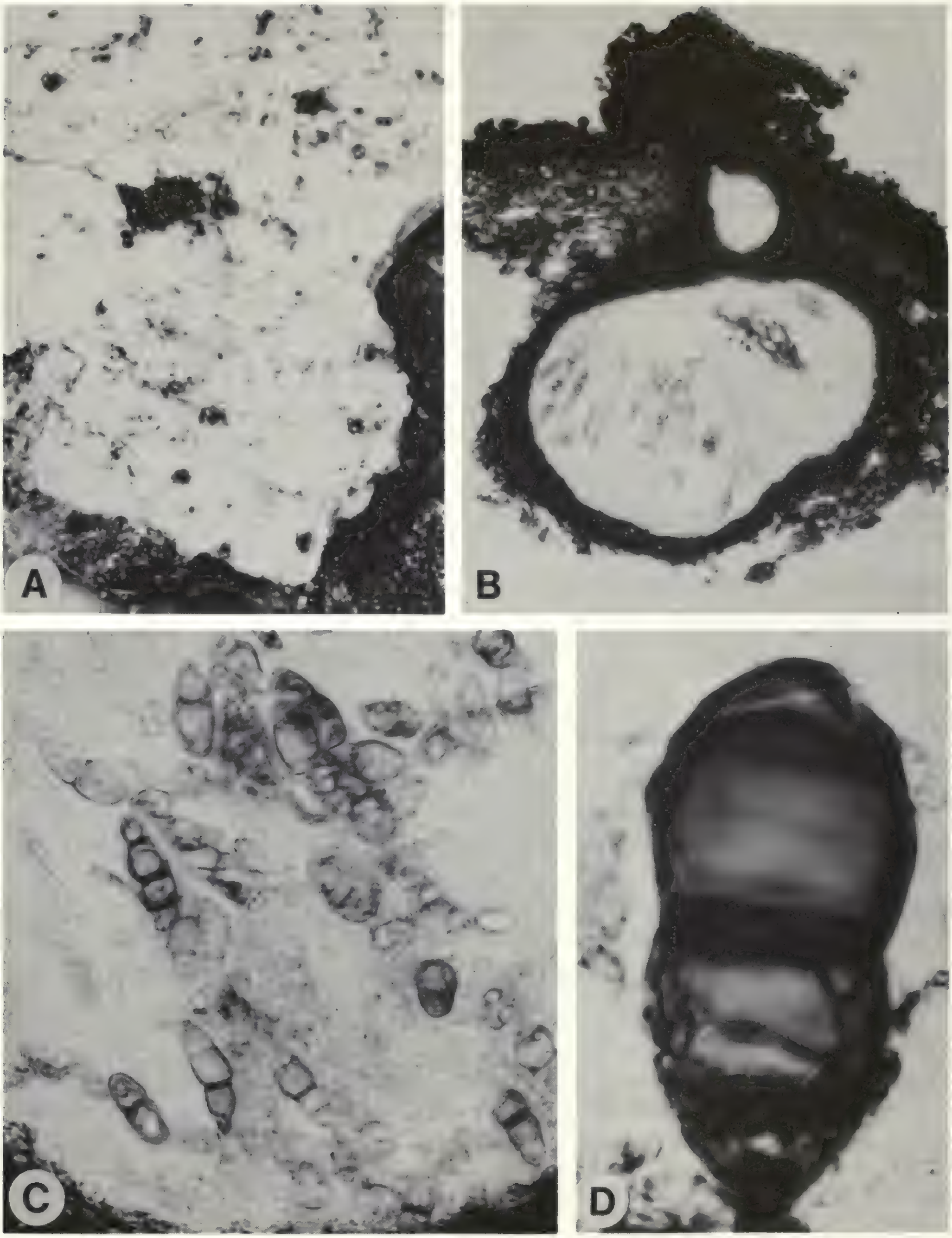

Fig. 55 *Verrucaria arctata* (BM—isotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma showing the distinct neck, × 80. **C**, Immature ascospores in the ascomatal cavity, × 800. **D**, Mature ascospore, × 2200.

Microtheliomyces atomariae (Ach.) Cif. & Tom. in *Atti Ist. bot. Univ. Lab. crittogam. Pavia* **10**: 59 (1953).

For numerous other obligate synonyms see Zahlbruckner (1921: 256, 272).

The nomenclature of this epithet is extremely complex as it has come to be used for two quite unrelated species, one belonging to *Leptorhaphis* and the other to *Mycomicrothelia*. This dichotomy has been recognized at least since the early 1850s (e.g. Körber, 1855) but evidently originated with De Candolle's misapplication of the epithet in 1805 (Lamarck & De Candolle, 1805: 313). That Acharius was dealing with the species also called *Verrucaria populicola* Nyl. (i.e. *Leptorhaphis tremulae* Körber) was firmly established by Vainio (1921*b*: 190) who studied Acharius' original material in H-ACH (the taxon is not represented in BM-ACH) and found that it produced hyaline, 3-septate, slightly arcuate ascospores measuring 22–24 × 3 μm.

In attempts to maintain the epithet in both genera, that in *Microthelia* has commonly been attributed to De Candolle (loc. cit.) but he cited '*Lichen atomarius* Ach. Lich. 16' so clearly did not intend to introduce a new taxon. As both taxa are not lichenized, by taking advantage of the later starting point date for Fungi caeteri (Art. 13) Hawksworth *et al.* (1980) continued the dual usage by amending the author citations. With the changes in Art. 13 abolishing later starting points effected at the Sydney Congress in 1981, however, such a procedure cannot be maintained and the epithet must be applied only in the sense of Acharius' type: i.e. in *Leptorhaphis* as the correct name for the species often called *L. tremulae*.

The correct name for the *Mycomicrothelia* species to which the epithet '*atomaria*' has commonly been misapplied is *M. melanospora* (see p. 95).

Microthelia atramentea Norman in *Bot. Notiser* **1867**: 88 (1867).

The holotype and several isotypes were studied by Hawksworth (1981*b*) who found this name to be a later synonym of *Lichenothelia scopularia* (Nyl.) D. Hawksw. For obligate synonyms of *M. atramentea* see Hawksworth (loc. cit.).

Microthelia atricola Lindsay in *Trans. R. Soc. Edinb.* **25**: 542 (1869).

Type: Ireland, Co. Kerry, Derriquin, on *Lecanora atra* (Huds.) Ach. on red sandstone, *T. Taylor* (not traced).

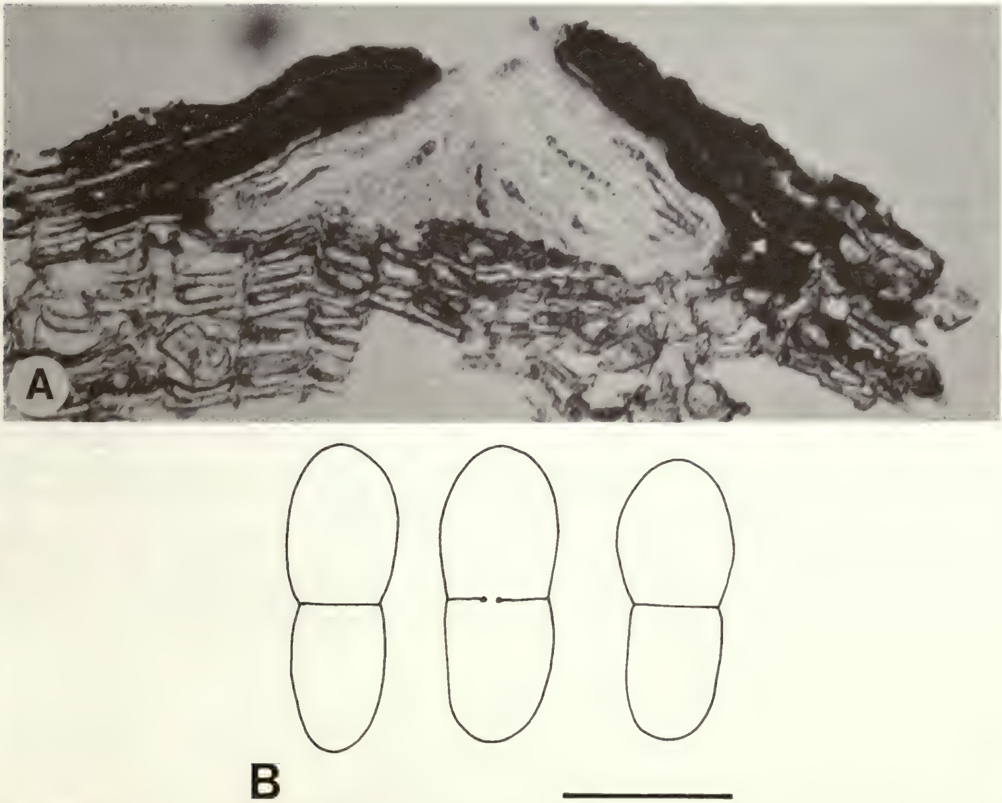

Fig. 56 *Microthelia asiatica* (TUR 32852—holotype). **A**, Vertical section of ascoma, × 250. **B**, Ascospore outlines, scale = 10 μm.

Muellerella atricola (Lindsay) Sacc. & D. Sacc., *Syll. Fung.* **17**: 594 (1905).
Endococcus atricola (Lindsay) H. Olivier in *Bull. Acad. internat. géogr. bot.* **17**: 125 (1907).

The original collection of this species was stated to be in 'Herb. Moore, Dublin' but it could not be located in DBN nor BM, E, or K. The asci were described as multispored, and the spores deep brown, simple, and globose. It seems probable that a *Muellerella* species was involved, perhaps one of the species in which the spores only become 1-septate at maturity (e.g. *M. lichenicola* (Sommerf. ex Fr.) D. Hawksw.), but some uncertainty must remain in the absence of the type material.

Microthelia aurora Zahlbr. in *Annls mycol.* **2**: 268 (1904).

Type: Java, Bogor Botanical Garden, on *Canariopsis decumanii*, *K. Giesenhagen* [Zahlbruckner, *Lich. rar. exs.* 43.] (W 1904/5218—holotype).

Fig. 57A–C.

This species is almost certainly congeneric with *M. macrocarpoides* (p. 155) and *M. hymenothora* (p. 150) on the basis of its ascospores, which are equal-celled and with characteristically very thick walls. The ascospores are 13–16 × 8·5–11 μm and the ascomata hemispherical, black with a purplish basal fringe, and (300–)400–500(–600) μm diam; no intact asci were seen. The thallus is pinkish and perhaps was lichenized but this was not clearly evident from the sections made. The ostiole is central in this species.

Microthelia baeomycearia Lindsay in *Trans. R. Soc. Edinb.* **25**: 541 (1869).

Type: British Isles, Perthshire, Balthayock Woods, on *Baeomyces rufus*, June, 1856, *W. L. Lindsay* (E—holotype).

On the basis of the original description and illustrations Hawksworth (1980*a*) treated this name as a later synonym of the species now known as *Pyrenidium actinellum* Nyl. (Hawksworth, 1983*a*). Dr B. J. Coppins recently discovered the holotype collection in E and examination of it confirmed this determination; the ascospores in the type measured 22–27 × 9–11 μm.

Microglaena biatorella Arnold in *Ver. zool.-bot. Ges. Wien* **23**: 501 (1873).

Microthelia biatorella (Arnold) Zahlbr., *Cat. Lich. Univ.* **1**: 189 (1921), as 'Dalla Torre et Sarnth.', nom. inval. (Art. 34.1).

Zahlbruckner (loc. cit.) indicated that Dalla Torre & Sarnthein (1902: 557) made a 'lapsus calami' and placed this epithet in *Microthelia*. Inspection of their work showed that they treated the species in *Microglaena* Körber, and that the 'lapsus' was not theirs' but was Zahlbruckner's! *M. biatorella* is a currently accepted species with hyaline muriform ascospores 30–45 × 14–17 μm (Poelt, 1969: 394) now placed in the monotypic genus *Leucocarpia* Vězda.

Verrucaria biformis Borrer *in* Hooker & Sowerby, *Engl. Bot.*, Suppl. **1**: tab. 2617 fig. 1 (1829).

Microthelia biformis (Borrer) Massal., *Misc. Lich.*: 58 (1856).
Anisomeridium biforme (Borrer) R. C. Harris *in* Vězda, *Lich. sel. exs.* 1503 (1978).

For further synonyms and typification see Swinscow (1970: 228). This is a hyaline-spored lichenized species correctly placed in *Anisomeridium* (Müll. Arg.) Choisy. Material erroneously considered to be conspecific with this species was distributed in Hepp, *Flecht. Eur.* exs. 108 (sub *Pyrenula biformis* (Leighton) Hepp) and contributed to Körber's (1855: 373) misinterpretation (see p. 157).

Müller & von Arx (1962: 284) attributed the epithet *biformis* to Leighton (1851: 37) but this procedure is unacceptable as Leighton himself unequivocably attributed it to Borrer. In any case Leighton's figure (loc. cit. pl. 15 fig. 2) is of a hyaline-spored species with the perithecia arising in a distinct thallus; Leighton examined material of Borrer's and appears to have correctly interpreted the species.

Verrucaria binucleolata Knight in *Trans. Linn. Soc. Lond.* **23**: 99 (1860).

Microthelia binucleolata (Knight) Müll. Arg. in *Bull. Herb. Boissier* II, **2** (App. 1): 93 (1894).

This species was described from a collection on bark collected by Knight in New Zealand, but detailed locality data and measurements were not provided. Unfortunately no material under this name was available from G and none appears to be present in WELT (P. J. Brownsey, in litt.).

As the species epithet indicates, guttule-like objects were an especial feature of this taxon and Knight (loc. cit., pl. 11 fig. 2) illustrated these clearly, also showing one spore with two locules and no septum. It

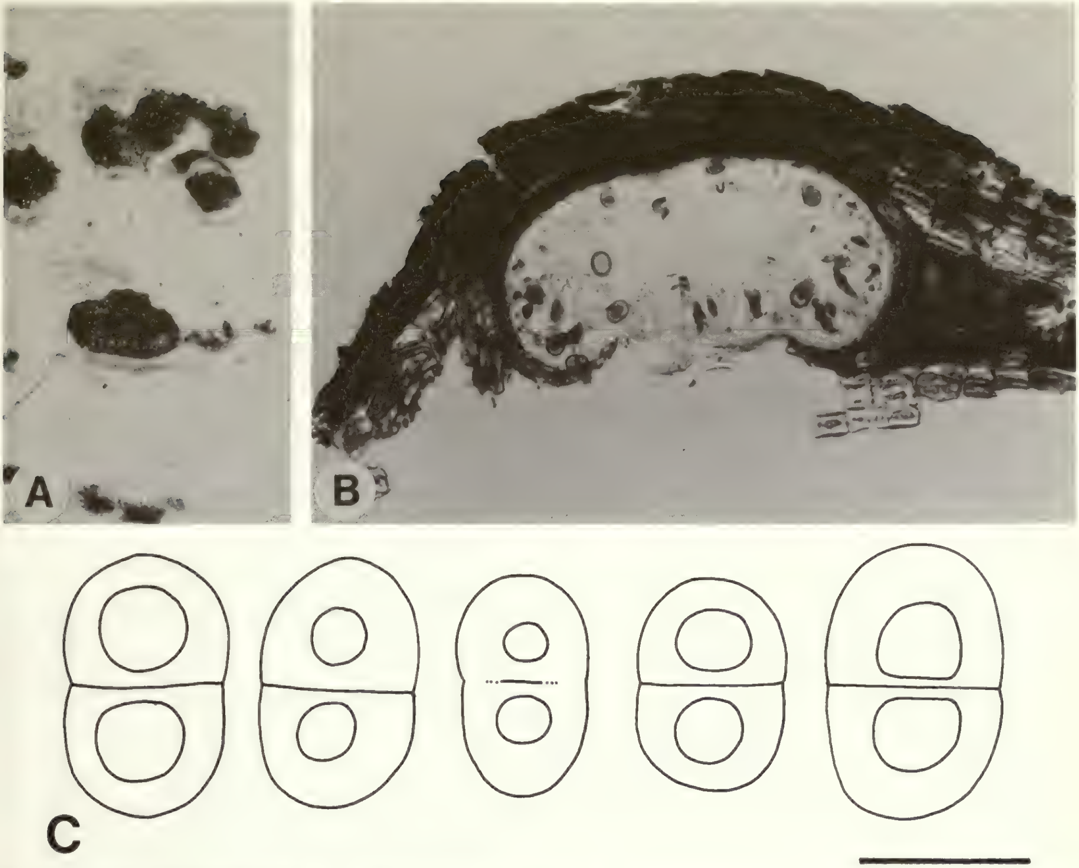

Fig. 57 *Microthelia aurora* (W 1904/5218—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

seems possible that Knight was dealing with a *Plagiocarpa* species (see p. 150), but in the absence of the type material the name must be treated as of uncertain application.

Microthelia calcaricola Mudd, *Man. Br. Lich.*: 306 (1861).

Type: 'Killing, Ireland, *Admiral Jones*', 'near Lewes, Sussex, *W. Unwin*' (syntypes, not traced).

Endococcus calcaricola (Mudd) Norman, *Sp. Loc. Nat. Norw.*: 375 (1868) [non vidi].
Tichothecium calcaricola (Mudd) Arnold in *Flora, Jena* **57**: 143 (1874).
Discothecium calcaricola (Mudd) Vouaux in *Bull. Soc. mycol. Fr.* **29**: 49 (1913).
Discothecium gemmiferum var. *calcaricola* (Mudd) Keissler, *Rabenh. Krypt.-Fl.* **8**: 389 (1930).
Endococcus calcareus Nyl. ex Crombie, *Lich. Br.*: 122 (1870), nom. illegit. (Art. 63.1).

Although the type material of this taxon could not be found, to judge from the original description and habitat it is almost certainly a later synonym of *Endococcus rugulosus* Nyl. (see p. 164).

Microthelia calyciospora Massal. in *Atti R. Ist. veneto Sci.* III, **2**: 377 (1857).

Type: [Italy ?; no locality data] (VER—holotype).

Arthopyrenia calyciospora Massal. in *Atti R. Ist. veneto Sci.* III, **2**: 337 (1857), as 'in litt. ad cl. Leighton 1855', nom. inval. (Art. 34.1).
Microthelia atomaria f. *calyciospora* (Massal.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 34 (1936).
Mycomicrothelia atomaria f. *calyciospora* (Massal.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 34 (1936).

Figs 58A, 60A.

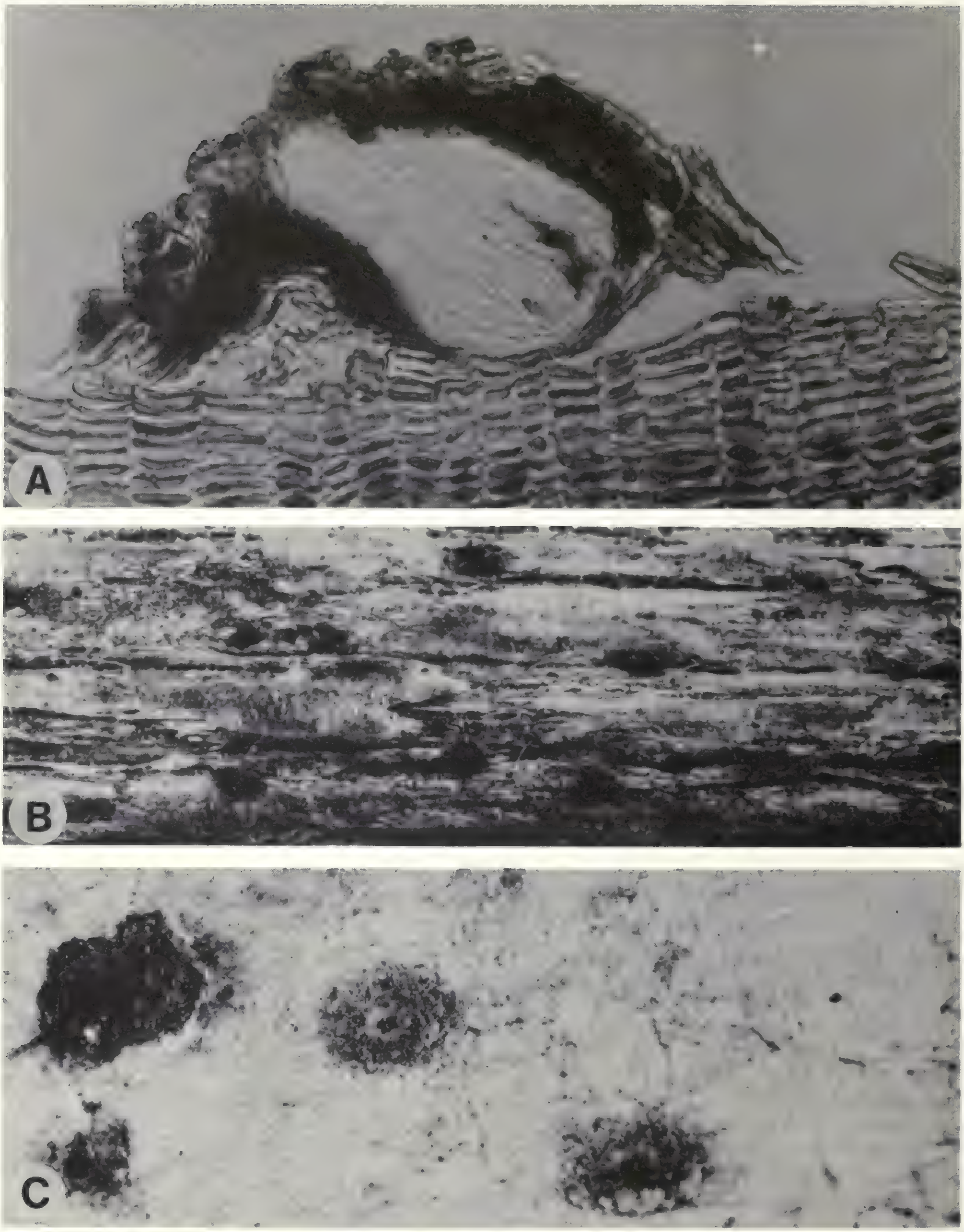

Fig. 58 **A**, *Microthelia calyciospora* (K), vertical section of ascoma, × 500. **B**, *Kirschsteiniella canariensis* (W 1978/10813—holotype), surface view, × 20. **C**, *Verrucaria clavaeformis* (BM—isotype), surface view, × 20.

The collection sent to Leighton in 1855 is present in K but is labelled as from 'Prov. Patavina', while when publishing the epithet in 1857 Massalongo gave the habitat and locality details as 'Ad ramulos juniores quercum in nemore *Montelo* prov. Tarvisinae (Massal.)'. In Massalongo's herbarium there are two unlocalized specimens under this epithet glued to the same sheet, but one of these has a 'B' and '*Arthop.* ? *calyciospoa* Massal.' by it. The unlettered specimen with no expression of doubt is considered as almost certainly the holotype despite the lack of further information. Both specimens in VER agree with each other and that in K; according to Keissler (1936: 34) the host is *Crataegus* in all cases but I have not checked the wood anatomy and Keissler may be incorrect.

The ascomata are immersed, mainly 60–125 μm wide, with a hyphal dark brown wall becoming clypeate around the consistently laterally inserted ostiole. The bitunicate asci are cylindrical, *c.* 65 × 8 μm, laterally positioned and contain eight uniseriately arranged ascospores which are brown, ellipsoid, 1-septate when mature, not constricted at the septum, apparently smooth-walled, and measure 7·5–10 × 4·5–6·5 μm. The paraphysoids are persistent, trabeculate, rather sparsely branched and anastomosing, and 1·5–2 μm wide. This fungus is evidently very closely related to *Didymosphaeria rubicola* Berl., but differs from that species in its smaller ascospores. As no similar fungus appears to have been previously described the new combination **Didymosphaeria calyciospora** (Massal.) D. Hawksw., **comb. nov.**, is made for Massalongo's fungus here.

Kirschsteiniella canariensis Petrak in *Annls mycol.* **32**: 370 (1934).

Type: Canary Islands, Teneriffe, near Guimar, 'auf dürren, entrindeten, holzigen Kräuterstengeln', 26 May 1926, *A. Ade* (W 1978/10813—holotype).

Fig. 58B.

Examination of the holotype showed that the ascospores of this non-lichenized fungus were hyaline when discharged from the asci, 1-septate, broadly fusiform, strongly constricted at the septum, and attenuated just before the apices, with granular walls and a gelatinous sheath, and measured 17–22 × 7–8 μm. The paraphyses are distinctly cellular (not trabeculate) and the ascomata dimidiate. The species clearly belongs in *Arthopyrenia* s. str. as interpreted by Harris (1975); the structure of the ascomata precludes a placement in *Didymella* Sacc. ex Sacc. I did not find any brownish spores in the slides I prepared but it is reasonable to suspect that Petrak discovered a few senescent ascospores still retained in the asci which had become slightly pigmented with age; this phenomenon is not uncommon in *Arthopyrenia* (see also p. 49). The tropical species of *Arthopyrenia* are so imperfectly understood that it would be premature to introduce a new combination based on Petrak's name here because an earlier epithet may well exist.

Microthelia cargillianum Lindsay in *Trans. R. Soc. Edinb.* **24**: 439 (1866).

Examination of the holotype by Hawksworth (1977) established that this was a coelomycete correctly called *Lichenoconium cargillianum* (Lindsay) D. Hawksw.

Microthelia cargilliana Lindsay in *Trans. R. Soc. Edinb.* **24**: 439 (1866).

Type: Italy, 'Auf Kalksteingrölle ober der Schlucht am Abhange unter dem Griesthalgletscher bei Schluderbach, 17 July 1882, *F. G. C. Arnold* [*Lich. exs.* 958] (M—lectotype).

Microthelia marmorata f. *cartilaginosa* (Arnold) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 44 (1936).

This species is rather close to *Polycoccum marmoratum* (Krempelh.) D. Hawksw. but differs in several important characters: the perithecioid ascomata are largely immersed in the substrate, open irregularly, the hymenial gelatine does not turn deep blue in iodine, the asci are almost cylindrical not elongate-clavate, and the ascospores much less distinctly rugulose. The ascospores in the holotype are 25–30 × 12–14 μm but Arnold indicated that they could reach 34 × 15 μm. This species is consequently transferred to *Polycoccum* as **Polycoccum cartilaginosum** (Arnold) D. Hawksw., **comb. nov.**

Arnold provided no description in 1886 but refers to an earlier publication (Arnold, 1876: 399) where the species was described as '*Microthelia marmorata* var.'. No material collected prior to 1876 is present in M but his exsiccate is suitable as a choice for the lectotype because it was collected prior to the publication of the epithet *cartilaginosa*.

In the lectotype, perithecia of the *Polycoccum* are scattered and, although not with a well-delimited thallus, are not clearly associated with a *Verrucaria* species present on the rock; I am thus uncertain as to whether this fungus is lichenized, lichenicolous, or taking over the algae from other species to become lichenized. It merits further study based on more extensive recent collections.

Kirschsteiniella ciferriana Petrak in *Annls mycol.* **30**: 191 (1932).

Type: Dominican Republic, Monte Christy, El Morro, on *Anastrophia rosei* twigs, July 1929, *R. Ciferri* 3761 (W-PETRAK 37104—holotype).

Fig. 71C–D, F.

This fungus appears to be very close to and possibly even conspecific with *Microthelia thelenula* and is discussed further under that species (p. 167).

Verrucaria cinerella Nyl. in *Annls Sci. nat., Bot.* IV, **3**: 174 (1855).

Type: Chile [sine loc.] (H-NYL p.m. 7413—lectotype).

Non *Verrucaria cinerella* Flotow ex Zwackh, *Lich. exs.* 37, 217 (1850), nom. inval. (Art. 32.1).
Non *Microthelia cinerella* Flotow ex Zwackh in *Flora, Jena* **45**: 566 (1862).

Nylander (loc. cit.) attributed the epithet *cinerella* to Flotow and cited Zwackh's exsiccate nos. 37 and 217. The material in that exsiccate belongs to *Mycomicrothelia melanospora* (see p. 96), but in providing a description for the first time Nylander mentioned a collection from Chile and stated that its spores were 32–36 × 9–11 μm. As the only syntype agreeing with the validating description is that from Chile this is the only acceptable choice for a lectotype; the epithet is then attributed to Nylander alone as this lectotypification excludes Flotow's concept of the taxon. The lectotype in H is a fragmentary specimen which appears to be lichenized and has largely immersed ascomata; no mature spores were found by me but the species is almost certainly close to *Mycomicrothelia thelena*, if not a further synonym of that name.

In combining *cinerella* into *Microthelia* Zwackh (loc. cit.) did not refer to Nylander's paper but did cite his exsiccata, gave the host as *Crataegus* or *Mespilus*, listed the epithets *atomaria* and *melanospora* as synonyms, and gave a description. The spore dimensions given by Zwackh (10–12 × 4–5 μm) are clearly rather small for *M. melanospora*, but this presumably represented only an error in calibration. It is therefore clear that his description excluded Nylander's concept of '*cinerella*' from *Microthelia cinerella*, and Zwackh must be treated as validating a separate species, here treated as a synonym of *Mycomicrothelia melanospora*.

This interpretation appears to reflect Nylander's own views as he later (Nylander, 1858: 61) gave the spore range for '*cinerella*' as 12–17 × 6–9 μm and accepted *thelena* as distinct. Nylander was evidently confused by this group as he subsequently (Nylander, 1861: 281–282) used *cinerella* to encompass not only the taxon now called *Mycomicrothelia melanospora*, but further *M. thelena*, *Peridiothelia fuliguncta*, and probably *P. grandiuscula*.

Verrucaria clavaeformis Stirton in *Proc. Phil. Soc. Glasgow* **11**: 320 (1879).

Type: India, [Kerala], 'Neilghieries Mts' [Nilgiri Hills], *G. Watt* (BM—isotype).

Microthelia clavaeformis (Stirton) Zahlbr., *Cat. Lich. Univ.* **1**: 258 (1921).

Figs 58C, 60C.

This material includes two pyrenocarpous species, an *Arthopyrenia* s. str. and *Mycomicrothelia nonensis* (see p. 105) which was also described from Watt's collections in the Nilgiri Hills. The *Arthopyrenia* element must be treated as that to which the name must be applied as in the original diagnosis the ascospores were stated to be strongly attenuate below and much larger than in the species here treated as *M. nonensis*. Stirton (loc. cit.) stated that the spores become fuscous, but I only found hyaline ascospores 20–24 × 4·5–5 μm with a distinct gelatinous sheath to 3 μm thick in potassium hydroxide. In addition the spores were consistently 3-septate, rather than 1-septate as indicated by Stirton, and his measurements of 30–38 × 10–13 μm would appear to be grossly exaggerated. A note on the isotype in the hand of Miss A. L. Smith indicates that she found the spores to be 23–31 μm in length.

The ascomata are immersed in a whitish thallus (? lichenized) and to 250 μm wide, with a spreading hyphal fringe extending for a further 200–300 μm around the erumpent ostioles. The *Arthopyrenia* species of India are very poorly known, but as this seems to be particularly distinctive, the new combination **Arthopyrenia clavaeformis** (Stirton) D. Hawksw., **comb. nov.**, is made to accommodate this fungus. A more critical treatment and description must await further material, because very few ascomata remain on the specimen studied.

Microthelia collemaria Lindsay in *Trans. R. Soc. Edinb.* **25**: 555 (1869).

Type: British Isles, Yorkshire, Cleveland, Ingleby, on walls, 1857, *W. Mudd* (E—holotype).

Tichothecium collemarium (Lindsay) Zopf in *Hedwigia* **35**: 324 (1896).

No description in writing accompanied the introduction of this name, but an illustration showing the diagnostic features was provided and so the name is accepted as validly published in accordance with Art. 44.1–2. Lindsay stated that the fungus was growing with '*Collema muscicolum*, Ach.', but in fact the fungus conforming to his illustration occurs on a sterile crustose lichen thallus mixed amongst *Leptogium teretiusculum* (Wallr.) Arnold. Examination of the holotype showed that the fungus was *Muellerella lichenicola* (Sommerf. ex Fr.) D. Hawksw. and Lindsay's epithet should consequently be added to the synonymy of that species (see Hawksworth, 1979*a*: 289).

Verrucaria confusa Garov., *Tent. Disp. Lich. Langob.*: 77 (1865).

Type: Germany, Heidelberg, on *Tilia*, 1849, *W. R. von H. Zwackh* [*Lich. Exs.* 37 (A)] (K—lectotype).

Fig. 60B.

Garovaglio's name was listed as a synonym of *Microthelia micula* by Zahlbruckner (1921: 262) and of *M. biformis* by Müller & von Arx (1962: 284). However, the above lectotypification, which is in agreement with the illustrations published by Garovaglio (loc. cit.: tab. 5 fig. 3), establishes the species as a member of the genus *Trematosphaeria* Fuckel, into which genus the species has been combined as *T. confusa* (Garov.) Boise & D. Hawksw. (*in* Boise, 1985: 232). *T. confusa* differs from *T. pertusa* (Pers.) Fuckel in the larger ascospores; the separation of these two species is discussed in detail by Boise (1985).

Sphaeropsis conica Lév. *in* Demidoff, *Voy. Russie Mérid.*: 112 (1842).

Sphaeria leveillei Durieu & Mont. *in* Montagne, *Syll. gen. crypt.*: 228 (1856), nom. illegit. (Art. 63.1).
Amphisphaeria conica (Lév.) Ces. & de Not. in *Comm. Soc. Crittog. ital.* **1**: 224 (1863).
Kirschsteiniella conica (Lév.) Petrak in *Sydowia* **7**: 57 (1953).

This species is the holotype of *Sphaeropsis* Lév., a genus originally considered by Léville to differ from *Sphaeria* Haller ex Fr. in lacking asci. The name was used in both Coelomycetes and Pyrenomycetes and has been rejected in the Code against both *Amphisphaeria* Ces. & de Not. nom. cons. and *Sphaeropsis* Sacc. nom. cons. (Voss *et al.*, 1983: 288, 298); *S. conica* Lév. is cited as the type of *Amphisphaeria* in the Code.

Müller & von Arx (1962: 691) reported that the type material of *Sphaeropsis conica* could not be found in PC but that other material filed under this name represented an ascomycete with completely mucilaginous asci, the identity of which was uncertain. The name *S. conica* is therefore of uncertain application.

In order to retain the generic name *Amphisphaeria* Ces. & de Not. for use in its currently accepted sense, Müller & von Arx (1962: 692) suggested that the lectotypification of the generic name with *A. umbrina* (Fr.) de Not. proposed by Petrak (1923: 326) be accepted. In order to regularise this under the Code, however, a formal proposal to change the listed type species of *Amphisphaeria* Ces. & de Not. nom. cons. has been made (Hawksworth & Sherwood, 1981).

Verrucaria conspurcans Durieu & Mont., *Expl. Sci. Algérie*, Bot. **1**: 291 (1849).

Type: Algeria, [Algérie], *M. C. Durieu de Maisonneuve* (PC—lectotype).

Microthelia conspurcans (Durieu & Mont.) Trevisan, *Consp. Verruc.*: 10 (1860).

Fig. 60D.

This name was placed as a synonym of *Verrucaria nigrescens* Pers. by Zahlbruckner (1921: 74) but examination of the two specimens on quartzitic sandstone (both localized only to country) in PC showed that no distinct thallus was present. The ascomata are perithecioid, compound, superficial, not leaving pits, black, 200–400 μm diam; the asci bitunicate, *c.* 80 × 22 μm, 8-spored; and the ascospores simple (*not* 1-septate), hyaline, ellipsoid, often slightly fusiform apically, distichously arranged in the asci, and 25–29 × 9–11 μm. This species was originally stated to have branched and anastomosing paraphyses but appears to have (a) abundant periphyses, and (b) occasional branched lateral pseudoparaphyses which are distinctly cellular and probably not anastomosing. It is very closely allied to *Verrucaria muralis* Ach. but differs in the larger ascospores.

This epithet was confused with *Arthopyrenia conspurcans* Th.Fr. by Keissler (1930: 355; 1936: 49), a lichenicolous fungus occurring on *Psora rubiformis* (Ach.) Hook., and consequently incorrectly listed as a synonym of the species now called *Stigmidium dispersum* (Lahm ex Körber) D. Hawksw.

Microthelia cookei Lindsay in *Trans. R. Soc. Edinb.* **25**: 537 (1869).

This taxon is a later synonym of *Muellerella lichenicola* (Sommerf. ex Fr.) D. Hawksw. (syn. *Tichothecium lichenicola* (Sommerf. ex Fr.) R. Sant.) as discussed by Hawksworth (1978*b*: 185), who studied the holotype and listed the obligate synonyms.

Pyrenula coryli Massal., *Rich. Auton. Lich. Crost.*: 164 (1852).

Microthelia glabrata var. *coryli* (Massal.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).
Mycopyrenula coryli (Massal.) Vainio in *Acta Soc. Fauna Fl. fenn.* **49** (2): 139 (1921).

For further synonyms, discussion, and illustrations see Keissler (1937: 393–397). *Mycopyrenula coryli* is the currently accepted name of this rare pyrenomycete of *Corylus* bark (and sometimes other smoothbarked trees, e.g. *Sorbus*), which produces brown 3-septate ascospores 10–17 × 4–6 μm in dimidiate compressed ascomata expanded laterally at the base. *Mycopyrenula* Vainio appears to be monotypic.

Microthelia crastophila Niessl in *Hedwigia* **21**: 84 (1882).

Didymosphaeria crastophila (Niessl) Winter, *Rabenh. Krypt.-Fl.* **1** (2): 422 (1887).
Massariopsis crastophila (Niessl) Kirschst. in *Annls mycol.* **33**: 218 (1935).

The original material on which this name was based was studied by Scheinpflug (1958: 341), who found it to be a later synonym of *Didymosphaeria futilis* (Berk. & Broome) Rehm.

Microthelia delitschia Niessl *in* Rehm, *Ascomyceten*: 943 (1888), nom. inval. (Art. 32.1).

On the leaves of *Sesleria caerulea* in Austria; to be treated in a revision of the foliicolous *Didymosphaeria*-like fungi.

Microthelia aterrima var. **dermatinoides** Servít in *Sber. K. böhm. Ges. Wiss., math.-nat. Kl.* **1929** (13): 16 (1930).

The type material was not available from PRM (M. Svrček, in litt.) but, according to the original description, this name is almost certainly a later synonym of the species now known as *Lichenothelia scopularia* (Nyl.) D. Hawksw.

Sphaeria diplospora Cooke in *J. Bot., Lond.* **4**: 102 (1866).

The combination '*Microthelia diplospora* (Cke.) Niessl' was mentioned by Scheinpflug (1958: 345) in a list of herbarium specimens, but the combination does not appear to have ever been validly published. Cooke's taxon is now regarded as a synonym of *Didymosphaeria oblitescens* (Berk. & Broome) Fuckel.

Microthelia dispora A. L. Sm. in *J. Bot., London.* **49**: 44 (1911).

Type: British Isles, Gloucestershire, Sapperton, Four Mile House, on *Verrucaria baldensis* Massal., *W. Joshua* (K—holotype).

Examination of the holotype confirmed that this name is a synonym of the species now known as *Polycoccum dzieduszyckii* (Boberski) D. Hawksw. (see p. 145). In the holotype of Smith's name the asci are 2-spored, and ascospores measuring 26–28 × 8–9 μm were noted; Smith (loc. cit.) gave their range as 25–35 × 10 μm, towards the lower end of the range for the species.

Verrucaria dissepta Nyl. in *Flora, Jena* **59**: 576 (1876).

Type: Ireland, 'Hibernia occid.', 1875, *C. du B. Larbalestier* (H-NYL 394—holotype).

Microthelia dissepta (Nyl.) A. L. Sm., *Monogr. Br. Lich.* **2**: 332 (1911).

The ascospores are 3-septate to submuriform, dark brown, verruculose, and 21–22 × 9·5–11·5 μm. The perithecia are erumpent from a lichen thallus that may well be *Rhizocarpon concentricum* (Davies) Beltr. (*R. petraeum* auct., non (Wulfen) Massal.). The species is probably conspecific with *Pleospora peripherica* (Taylor) D. Hawksw. (see p. 159), but differs in the slightly wider ascospores.

Microthelia dominans Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **30** (3): 38 (1888).

Type: [sine loc.], 'cortex *Crotonis cascarillae*', ex hb. Fée (G—holotype).

Fig. 59A–B.

The holotype consists of two small pieces of bark with a single ascoma on each; a third was used to prepare microtome sections retained in IMI. The ascomata are 300–400 μm diam, black, shining, pseudostromatic and dimidiate, with trabeculate pseudoparaphyses to *c.* 1·5 μm thick, and forming (1–)3(–5) septate ascospores measuring 35–40 × 12·5–13 μm. According to the original description the ascospores may be 32–46 × 11–16 μm. The walls of the ascospores are verruculose. This taxon is close to that described as *M. thelena* var. *albicans* (see p. 130), but differs in the somewhat larger ascospores.

Microthelia donacina Niessl *in* von Thümen, *Instituto Coimbra* **28**: 31 [reprint] (1881).

Didymosphaeria donacina (Niessl) Sacc., *Syll. Fung.* **1**: 715 (1882).

This species was accepted in *Didymosphaeria* by Scheinpflug (1958: 358), and an examination of collections referred to this primarily bambusicolous and graminicolous species confirmed that it should be retained in that genus as currently circumscribed; the ascomata are immersed, with well developed ostioles, and entire with the walls composed of mainly hyaline pseudoparenchymatous cells, becoming brownish only around the ostiole. The 1(–3)-septate ascospores are rather pale brown and given by Scheinpflug as 12–17 × 4–5 μm.

Microthelia dotyi Herre in *Bryologist* **56**: 279 (1953).

Type: Polynesia, Tuamoto, Raroia Atoll, 'probably . . . on *Cocous* [sic] *nucifera*', 1952, *M. S. Doty & J. Newhouse* (not traced).

This species was described as forming very large ascomata 0·4–0·9 mm wide, cylindrical extremely narrow asci 56–77 × 5–6 μm, and uniseriately arranged ascospores which were brown, 1-septate, and 9–13 × 3·5–5·5 μm. Material utilized was stated in the introduction to be distributed between the Bishop Museum in Honolulu (BISH) and Herre's own herbarium (now in F). Unfortunately the collection could not be located in BISH (S. H. Sohmer, in litt.) and no reply was received to a request for it from F. According to the original description, it seems most unlikely that this taxon belongs to any of the genera accepted in the main body of the present revision. The uniseriately arranged ascospores and long and narrow asci are suggestive of *Didymosphaeria* s. str., but such massive ascomata and a whitish superficial thallus almost certainly preclude its placement there. If the material is refound, especial attention should be paid to the structure of the asci and the paraphyses, which may help fix the position of this evidently most interesting taxon.

Microthelia dzieduszyckii Boberski in *Spraw. Kom. fizyogr. Kraków* **22** (2): 68 (1888).

Phaeospora parasitica f. *dzieduszyckii* (Boberski) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 50 (1936).
Polycoccum dzieduszyckii (Boberski) D. Hawksw. *in* Hawksworth, James & Coppins in *Lichenologist* **12**: 107 (1980).

Although no authentic material of this taxon is available, the original description leaves little doubt that Boberski was dealing with the *Polycoccum* species for which his epithet has been used by recent authors. The ascospores were originally stated to be 34–44 × 12–14 μm and 'constanter duae in asco'. Boberski (loc. cit.) further indicated that his fungus was associated with calcicolous crustose lichens, the usual hosts for this fungus.

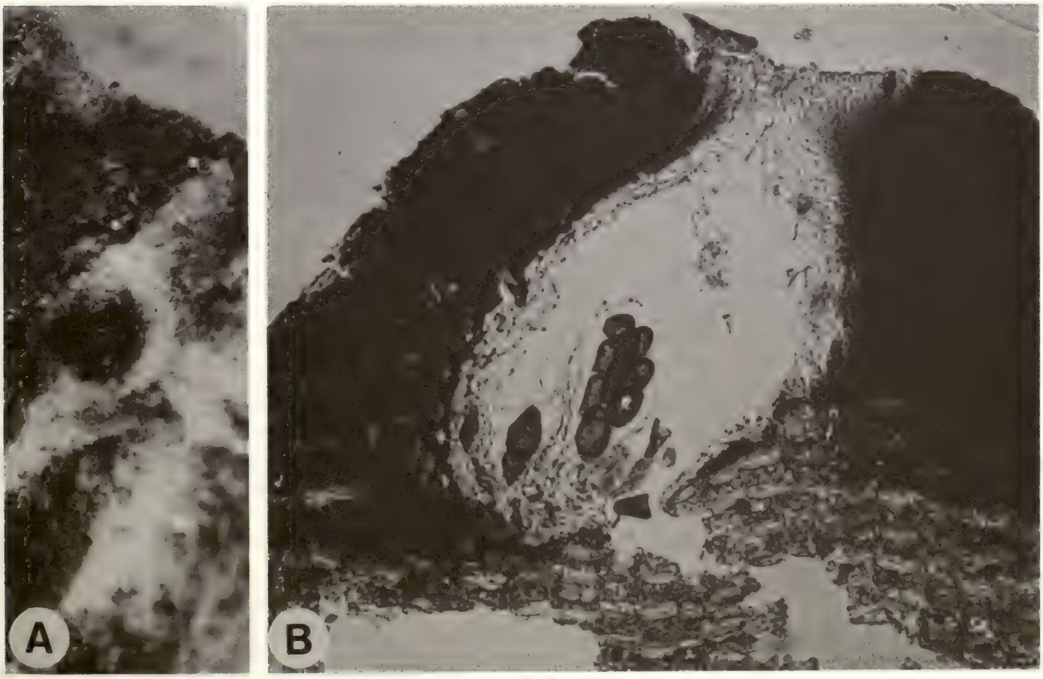

Fig. 59 *Microthelia dominans* (G—holotype). **A**, Surface view, × 20; **B**, Vertical section of ascoma, × 250.

Microthelia ecatonspora Anzi in *Atti Soc. ital. Sci. nat.* **9**: 256 (1866).

Type: Italy, 'ad rupes calcareas montis Parete (in alpibus Rhaeticis)', *M. Anzi* [*Lich. rar. Langob.* exs. 489] (BM—isotype).

For obligate synonyms see Keissler (1930: 414).

Examination of the isotype established that this name is a further synonym of the species now known as *Muellerella lichenicola* (Sommerf. ex Fr.) D. Hawksw. (see Hawksworth, 1979*a*: 289).

Microthelia elata Harm. in *Bull. Séanc. Soc. Sci. Nancy* III, **12**: 138 (1911).

No material under this name could be located in the Harmand herbarium at Angers (M. Guerlesquin, in litt.). It was described from bark in New Caledonia on the basis of material collected by R. P. Pionnier and had dimidiate ascomata 0·4–0·7 mm diam, 8-spored asci, distichously arranged spores, and the spores themselves appear to have been verruculose and 18 × 7–7·5 μm; pycnidia forming bacilliform conidia 4–5 × 0·8 μm were also mentioned in the original description. The ascospore measurements are suggestive of *Mycomicrothelia pachnea* (see p. 108) but the much larger ascomtanata of Harmand's species indicate it cannot belong there. Perhaps a distinct species but in the absence of material it can only be treated here as of uncertain application.

Micropeltis erumpens Berk. & Curtis *in* Berkeley in *J. Linn. Soc. Lond.* **10**: 375 (1868).

Type: Cuba, on palm petioles, February, *C. Wright* 474, 556 (K—syntypes).

Pemphidium erumpens (Berk. & Curtis) Sacc., *Syll. Fung.* **2**: 670 (1883).
Astrosphaeriella erumpens (Berk. & Curtis) Theiss. in *Annls mycol.* **14**: 436 (1916).
Microthelia erumpens (Berk. & Curtis) Speg. in *Boln Acad. Cienc. Córdoba* **26**: 384 (1923) [pre-print].
Seynesia erumpens (Berk. & Curtis) Petrak in *Annls mycol.* **25**: 339 (1927).

For further synonyms, detailed description, and illustration see Müller & von Arx (1962: 696).

Examination of the syntypes in K confirmed that this species had unitunicate asci with refractive apical cylinders turning deep blue in iodine solution, and simple filiform paraphyses. This is a typical member of the Sphaeriales, though the subepidermal habit superficially recalls *Astrosphaeriella aosimensis* (see p. 134).

The species is clearly quite remote from the other taxa accepted in the present revision and can be conveniently retained in the monotypic genus *Seynesia* Sacc.

Phaeothyriolum eucalyptinum H. Sydow in *Annls mycol.* **36:** 305 (1938).

Type: Australia, New South Wales, Barrington Tops, 'in foliis *Eucalypti pauciflorae*', 7 January 1934, *L. Fraser* 133 (not traced).

Mycomicrothelia eucalyptinum (H. Sydow) E. Müller *in* Müller & von Arx, *Beitr. Kryptog.-fl. Schweiz* **11** (2): 327 (1962).

Material of this leaf-inhabiting species is not available from S (Å. Strid, in litt.) and I am not convinced that it should be placed in *Mycomicrothelia* on the basis of the original description alone. The species is said to produce subcuticular ascomata in groups 0·5–1·5 mm wide, individually 100–180 μm but forming confluent crusts. The asci are reported as 40–55 × 15–18 μm, 8-spored, and the ascospores as oblong-clavate, centrally 1-septate, not or slightly constricted at the septum, usually rounded at the apices, at first hyaline but later pellucid olivaceous-brown, and 15–17 × 5–7 μm in size. Sydow indicated that the paraphyses were yellowish brown.

Endococcus exerrans Nyl. in *Flora, Jena* **62**: 360 (1879).

Microthelia exerrans (Nyl.) A. L. Sm., *Monogr. Br. Lich.* **2**: 232 (1911).

The holotype and several isotypes were studied by Hawksworth (1979*a*) who found this to be an acceptable species of *Endococcus* Nyl.

Verrucaria farrea Ach., *Meth. Lich.*: 115 (1803).

Microthelia farrea (Ach.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903).

For further obligate synonyms see Keissler (1937: 400–401).

This name has often been cited (e.g. Keissler, 1937; Zahlbruckner, 1922) as a probable synonym of the species now known as *Eopyrenula leucoplaca* (Wallr.) R. C. Harris, a species which produces brown fusiform ascospores which are 5–6-septate and measure 18–24 × 5–9 μm (Harris, 1973: 20).

Vainio (1921*b*: 144) examined the original material of Swartz on which Acharius based this epithet in H, and reported that there were two specimens which had colourless simple spores. In BM-ACH 309 there are three specimens on lignum under this name; two are of an unidentified *Lecidea* species (with colourless simple spores), and the third is a pyrenomycete with a whitish 'thallus', ascomata 200–300 μm diam, clavate 8-spored asci, a centrum turning blue in iodine, and producing hyaline 3-septate broadly ellipsoid spores 28–33 × 14_16 μm; the identity of the latter is uncertain.

Arthopyrenia furfuracea Massal. in *Lotos* **6**: 82 (1856).

Type: Italy, Verona, Tregnago, 'ad truncos pruni Cerasi', *A. B. Massalongo* [Anzi, *Lich. rar. Venet.* exs. 124] (BM—isotype).

Verrucaria micula var. *furfuracea* (Massal.) Garov., *Tent. Disp. Lich. Langob.*: 79 (1865).
Microthelia furfuracea (Massal.) Bagl. & Car. in *Atti Soc. Crittogam. Ital.* **2**: 338 (1881).
Microthelia micula b. [f.] *furfuracea* (Massal.) Jatta, *Syll. Lich. Ital.*: 555 (1900).

Fig. 60E.

When mature the ascomata in this non-lichenized species have an exposed hymenium and appear lecideine in surface view. The asci are bitunicate, not reacting with iodine, and borne in a dense mass of branched and anastomosing true cellular pseudoparaphyses which grow downwards from the tissue which later forms the excipulum. The ascospores become pale brown and are weakly verruculose when mature, measuring 19–25 × 8·5–11 μm. Keissler (1936: 53) indicated that this species was identical with *Melaspilea proximella* (Nyl.) Nyl. ex Norrlin, but if the figures of Smith (1926: pl. 27) are correct this is definitely not so. The fungus could be accommodated in the heterogeneous genus *Melaspilea* Nyl., as currently interpreted, but I am not proposing any new combination here as *A. furfuracea* may not be congeneric with the type species of *Melaspilea, M. arthonioides* (Massal.) Nyl.* (see Müller & v. Arx, 1962: 258–9).

Astrosphaeriella fuscomaculans Yamamoto *in* Yamamoto, Maeda & Oyasu in *Sci. Repts Hyōgo Univ. Agric.* (Agric.) **1**: 63 (1954).

Microthelia fuscomaculans (Yamamoto) E. Müller *in* Müller & von Arx, *Beitr. Kryptog.-fl. Schweiz* **11** (2): 286 (1962).

The type material of this species was almost certainly destroyed when Yamamoto retired from Hyōgo University (Y. Doi, in litt.), but from the original description it seems that it is almost certainly a later synonym of *Astrosphaeriella stellata* (Pat.) Sacc. (see Hawksworth, 1981*a*).

Astrosphaeriella fusispora Sydow in *Annls mycol.* **11**: 260 (1913).

Microthelia fusispora (Sydow) E. Müller *in* Müller & von Arx, *Beitr. Kryptog.-fl. Schweiz* **11** (2): 285 (1962).

The holotype of this species, the type of *Astrosphaeriella* Sydow (see p. 53) was examined by Hawksworth (1981*a*) and found to be conspecific with the species correctly called *A. stellata* (Pat.) Sacc.

Verrucaria gemmifera Taylor *in* Mackay, *Fl. Hib.* **2**: 95 (1836).

Microthelia gemmifera (Taylor) Mudd, *Man. Br. Lich.*: 307 (1861).

For numerous other obligate synonyms see Keissler (1930: 385–386). The typification of this species was investigated by Hawksworth (1979*b*), who concluded that it must be rejected as the name was based on discordant elements (several different lichenicolous fungi), none of which could be selected as a satisfactory type. The epithet *'gemmiferum'* has been most widely used for the species now known as *Endococcus propinquus* (see p. 160).

Verrucaria glabrata Ach., *Syn. Lich.*: 91 (1814), nom. illegit. (Art. 63.1).

Microthelia glabrata (Ach.) Boistel, *Nouv. Fl. Lich.* **2**: 288 (1903), nom. illegit. (Art. 63.1).

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* Usually cited as '(Fée)Nyl.' but the basionym *Lecidea arthonioides* Fée is a later homonym of *Lecidea arthonioides* Ach. (i.e. *Arthonia arthonioides* (Ach.) A. L. Sm.). By the application of Art. 72. Note 1, the taxon in *Melaspilea* must be attributed to '(Massal.)Nyl.' (syn. *Catillaria arthonioides* Massal.). These two epithets appear to have been confused by Farr *et al.* (1979: 1064, 1774), with the result that it is implied that *Trachylia* Fr. is based on the same type as *Melaspilea*, which is incorrect.

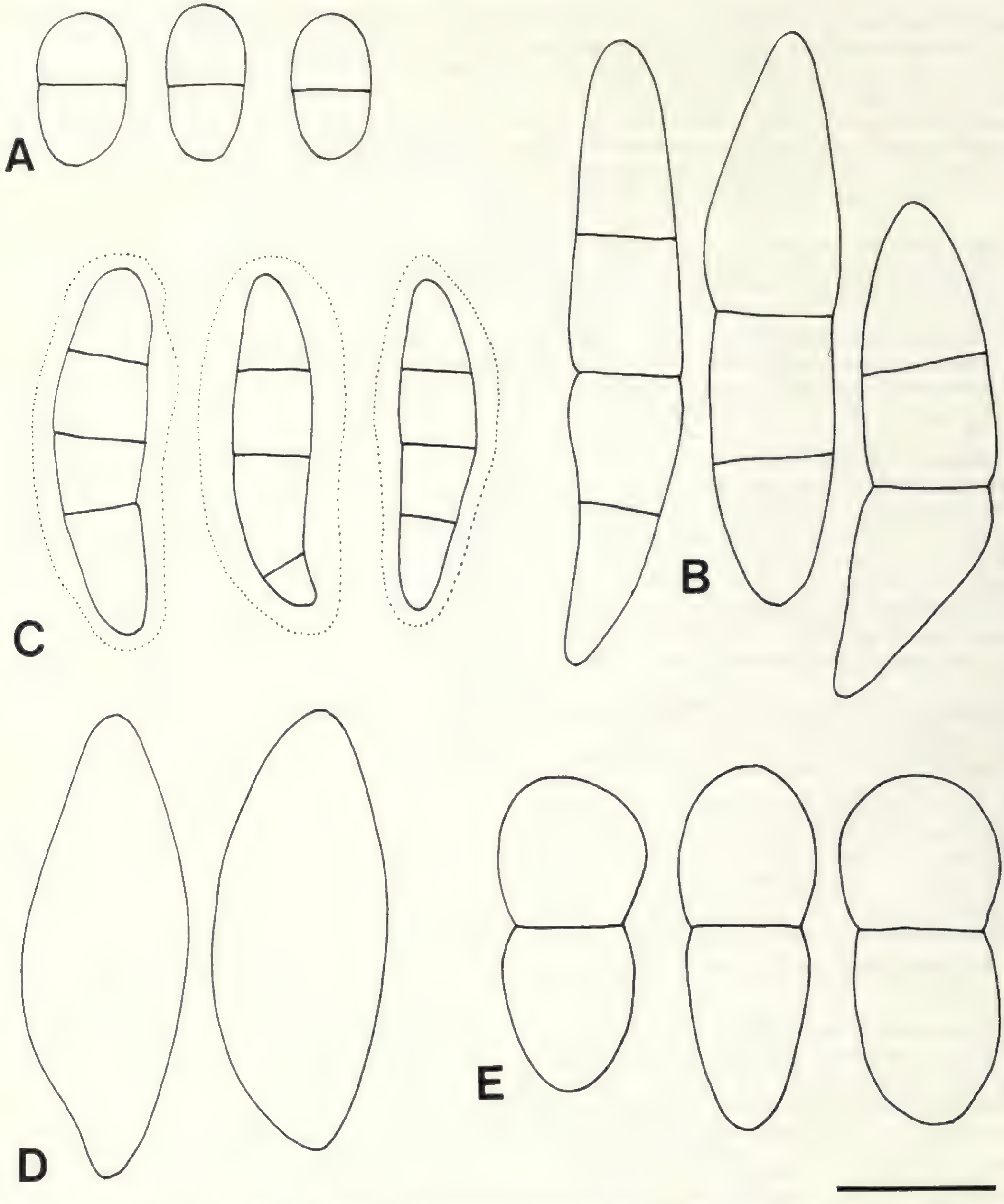

Fig. 60 Ascospore outlines. **A**, *Microthelia calyciospora* (VER—holotype). **B**, *Verrucaria confusa* (K—lectotype). **C**, *V. clavaeformis* (BM—isotype). **D**, *V. conspurcans* (PC—lectotype). **E**, *Arthopyrenia furfuracea* (BM—isotype). Scale = 10 μm.

When this epithet was first introduced, *Verrucaria laevigata* Pers. was cited as a synonym. Acharius' name is therefore automatically typified by the type of *V. laevigata* (Art 7.11), and is an obligate synonym of the species now known as *Pyrenula laevigata* (Pers.) Arnold.

Verrucaria guayci Fée, *Essai Crypt. Off. Suppl.*: 85 (1837).

Type: 'ad corticem *Guayaci officinalis*', hb. Fée (G—holotype).

Microthelia guayaci (Fée) Trevisan, *Consp. Verruc.*: 10 (1860).
Pyrenula guayaci (Fée) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **30** (3): 32 (1888).

Fig. 61A–C.

This is a 1-septate spored *Pyrenula*-like fungus with strongly thickened inner walls to the spores which have angular lumina. It is further characterized by the pale ascospores being mainly 17–25 × 8·5–9 μm and elongate-ellipsoid; over-mature (?) massive ascospores measuring 35–56 × 17–21 μm in which no septa are visible are also occasionally formed. In the absence of a monograph of the tropical Pyrenulaceae it is appropriate to retain this species in *Pyrenula* for the present.

Microthelia haplospora Norman in *Ofvers. K. VetenskAkad. Förh. Stockh.* **41** (8): 37 (1884).
Didymosphaeria haplospora (Norman) Vainio in *Acta Soc. Fauna Fl.fenn.* **49** (2): 151 (1921).

The original locality was given as '. . . pluribi prope Larvik et alibi ad corticem populi'. There are five collections of Norman's in O, of which four are from the Larvik district and one is labelled Rödosgn; none are present in TRH (S. Sivertsen, in litt.). All five packets include *Amphisphaerella dispersella* (Nyl.) O.

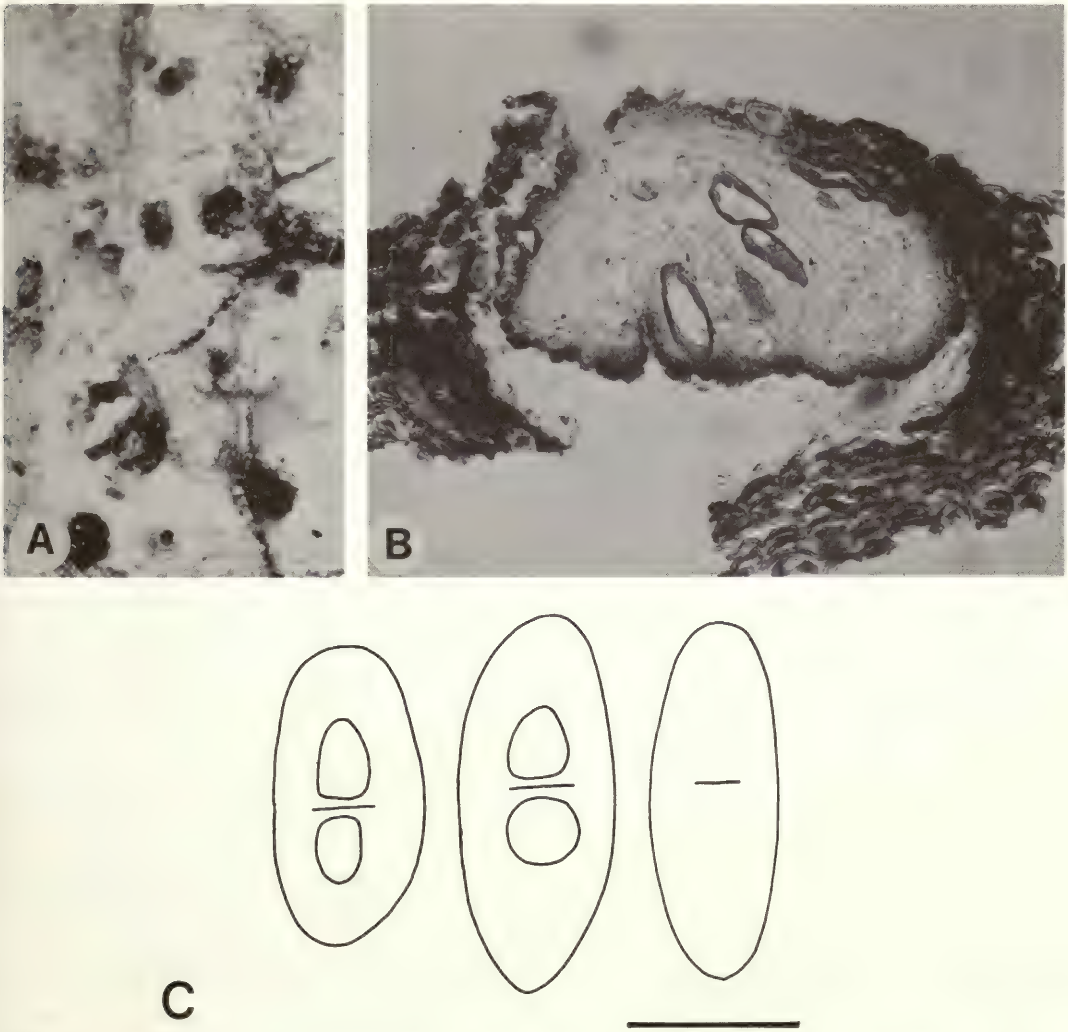

Fig. 61 *Verrucaria guayci* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

Eriksson (syn. *A. amphisphaerioides* (Sacc. & Speg.) Kirschst.)*, a very distinctive pyrenomycete with brown spores, each with 3 equatorial germ pores, 18–21 × 9–11 μm, borne uniseriately in the asci; at low magnification the equatorial pores give the ascospores the appearance of being 1-septate. Three of the Larvik specimens, including the only one with a date (Fredriksvass . . ., 1877, *J. M. Norman*, O), also support a second pyrenomycete with a lateral ostiole and red-brown spores 17–19 × 7·5–10 μm uniseriately arranged in the asci. The perithecial measurements given by Norman are applicable to the *Amphisphaerella* (which is most conspicuous), as is his description of the paraphyses as '. . . gelatinosae, guttulosae vel diffluentes' (the other fungus has conspicuous trabeculate persistent paraphysoids). He did, however, give the ascospores as 15–18 × 7–8 μm, but on the specimen from Rödosgn is a drawing with what are clearly the *Amphisphaerella* spores and '12 μ' by them; his ascospore measurements were evidently inaccurate. This latter collection shows unequivocably that Norman regarded the *Amphisphaerella* as his fungus, while there is no evidence that he regarded that with the lateral ostiole as at all allied to it. Norman's epithet is here lectotypified by the *Amphisphaerella* element in the 1877 collection and therefore becomes a later synonym of *A. dispersella*.

The fungus with a lateral ostiole is very close to, if not identical with, *Didymosphaeria rubicola* Berl.; that fungus is also present, with other fungi, on a specimen of Norman's labelled as *M. haplospora* in M from 'Laurvik: Andvik' and sent to Arnold by Norman in 1886.

Microthelia heterospora Eitner in *Jber. schles. Ges. vaterl. Kult.* **88** (2): 55 (1911).

The type material in WRSL was studied by Keissler (1936: 52) who found it to consist of *Hymenelia lacustris* (With.) Poelt & Vězda (syn. *Aspicilia lacustris* (With.) Th. Fr.) supporting a lichenicolous fungus he considered to be conspecific with *Pharcidia lacustris* (Arnold) Zopf. According to Eitner's description, his fungus had ascomata 100–200 μm wide and produced ascospores of two types: hyaline and 30 × 9–11 μm and brown and 30–34 × 12–14 μm.

Verrucaria holopolia Nyl. in *Bull. Soc. linn. Normand.* II, **2**: 131 [p. 92 of reprint] (1868).

Microthelia holopolia (Nyl.) Müll. Arg. in *Flora, Jena* **68**: 333 (1885).

This species, described from bark in New Caledonia, was reported to have 'paraphyses graciles' and massive ascospores 60–70 × 18–27 μm 'incolores (vel interdum fuscentes)'. The name is of uncertain application but it is most unlikely that the taxon belongs to any of the genera accepted in this paper.

Verrucaria hymenothora Ach., *Lich. Univ.*: 280 (1810).

Type: 'e *Bignonia triphylla* Amer.' (BM-Ach. s.n.—isotype).

Microthelia hymenothora (Ach.) Trevisan, *Consp. Verruc.*: 10 (1860).

Fig. 62A–C.

The isotype in BM consists of a perhaps non-lichenized pyrenomycete, entirely immersed in the outer layers of the bark, with a long, eccentric ostiole which is only erumpent at the apex, and sparsely branched septate paraphyses 2–3 μm wide. The thin-walled asci produce very unusual ascospores which are broadly ellipsoid, thick-walled with two locules, appearing almost polarilocular, eventually becoming incompletely 1-septate, slightly to not constricted at the septum, golden brown, slightly roughened, and measuring 12–17 × 7–11 μm. The hymenial gelatin turns blue in iodine. It is possible that this could be the same as *Valsaria bignoniae* (Schwein.) Cooke, described as having ascospores about 15 × 8 μm; that species was, however, said to have a distinct stroma, which *V. hymenothora* does not.

The fungus illustrated under this name by Eschweiler (1824: fig. 13a–b) is quite unlike the material in BM-Ach. in having dimidiate ascomata, a central ostiole, and 3-septate ascospores; Eschweiler's drawing may have been the reason why Trevisan placed the taxon in *Microthelia*.

The ascomatal structure is reminiscent of *Plagiocarpa* R. Harris and, although the asci have little apical structure at maturity, when young they appear to have the peculiarly shaped internal apical beak characteristic of that genus. However, the ascospores of that genus are multiseptate and lack the distinctively thickened inner walls. This species could however, through its 1-septate spores and eccentric ostiole, provide a link between *P. macrocarpoides* (see p. 153) and the multi-septate species of the genus. The group does, however, require further critical study before *V. hymenothora*, *Microthelia aurora*, and *M. macrocarpoides* can be transferred with confidence.

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* An additional synonym of this species is *Amphisphaeria emiliana* Fabre (*Annls Sci. nat.* (Bot.), VI, **9**: 85, 1878), confirmed by examination of the type material in the Fabre herbarium at L'Harmas (France: Vaucluse, on *Populus*, *J. H. C. Fabre*).

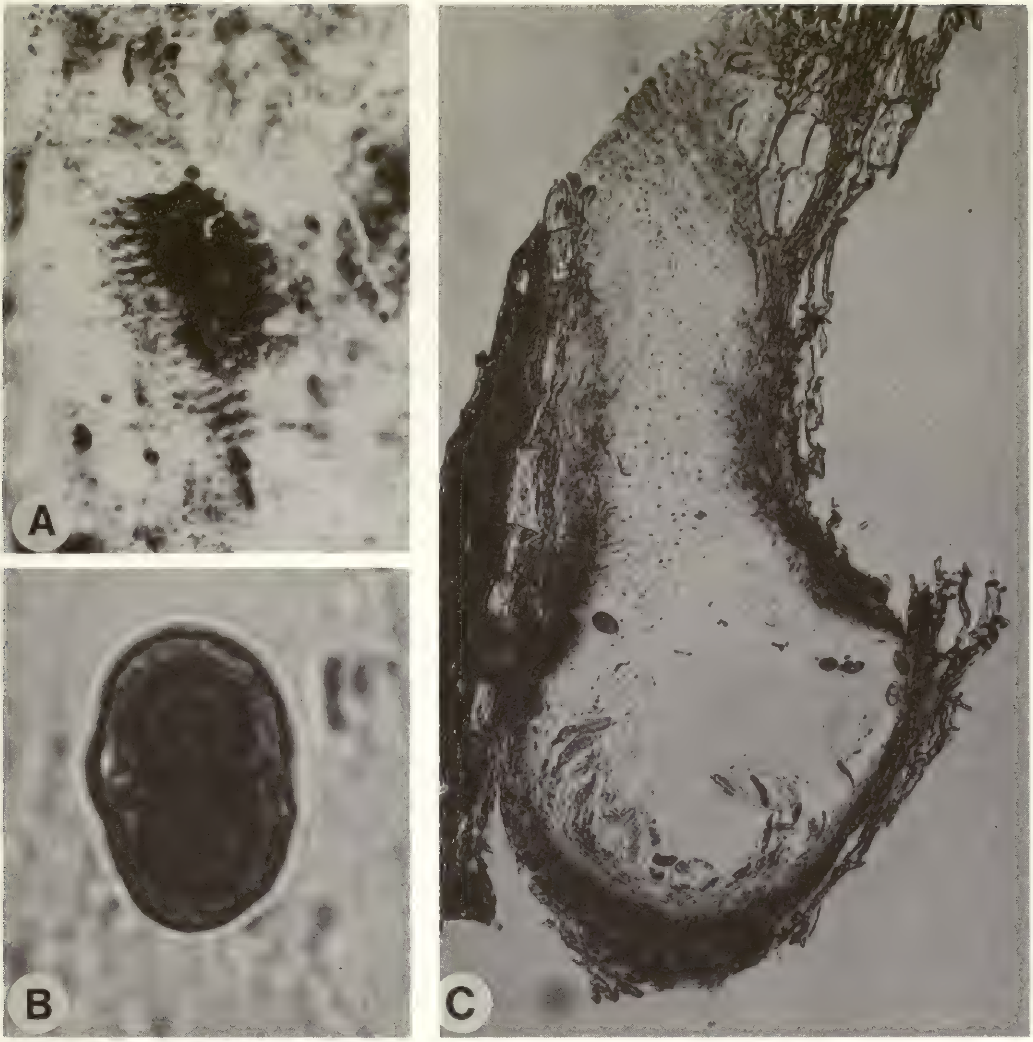

Fig. 62 *Verrucaria hymenothora* (BM-ACH—isotype). **A**, Surface view, × 56. **B**, Ascospore, × 2500. **C**, Vertical section of ascoma showing the long neck, × 250.

Amphisphaeria incrustans J. B. Ellis & Everh., *N. American Pyren.*: 201 (1892).

Microthelia incrustans (J. B. Ellis & Everh.) Corlett & S. Hughes *in* Hughes in *NZ. Jl Bot.* **16**: 360 (1978).

The holotype was studied by Hawksworth (1985*a*) who found this species was a synonym of *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw.

Microthelia innata Müll. Arg. in *Bot. Jb.* **6**: 417 (1885).

Type: Cuba, *sine loc.*, *C. Wright* [*Verr. Cub.* exs. 231] (G—holotype).

Fig. 63A–C.

Thallus crustose, effuse, thick, the surface smooth and almost shining, not cracked or areolate, pale ochraceus but whitish within, lacking a prothallus. *Ascomata* almost entirely immersed in the thallus with only the tip of the ostiole visible, scattered, occasionally aggregated but mostly rather evenly distributed, 75–120(–150) μm diam in surface view, 100–150 μm tall and mainly 100–120 μm wide in vertical section, rather irregular in shape but mainly subglobose to obpyriform, lacking an involucrellum, wall not

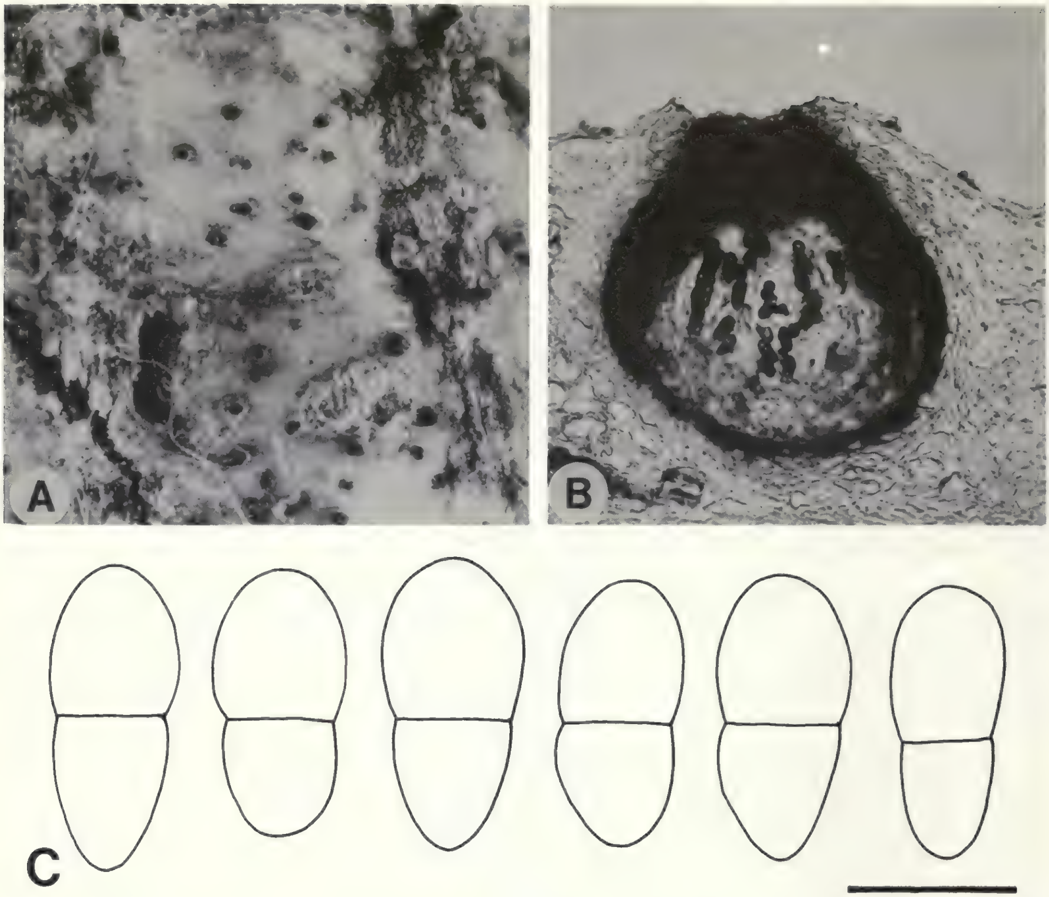

Fig. 63 *Microthelia innata* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascospore outlines, scale = 10 μm.

composed of bark cells intertwined with fungal hyphae, black; peridium ± entire but thicker on the upper sides and thinner at the base, mainly about 15 μm thick but becoming thicker near the ostiole where it may be as much as 30 μm thick in places, dark red brown, composed of densely compacted interwoven hyphae mainly 2·5–3·5 μm thick forming a textura intricata but in the vicinity of the ostiole appearing almost pseudoparenchymatous; centrum not turning blue in iodine. *Pseudoparaphyses* persistent, abundant, sparsely septate, richly branched and anastomosing. 1·5–2 μm thick. *Asci* elongate clavate, vertically orientated, bitunicate, 8-spored, fully mature asci not seen. *Ascospores* apparently distichously arranged in the asci, broadly ellipsoid, 1-septate, constricted at the septum, rounded to slightly attenuated at the apices, cells almost equal in size or the lower slightly smaller, brown, verruculose to almost smooth-walled, with a gelatinous sheath sometimes swelling markedly in potassium hydroxide, (15–)16–18(–19) × (6·5–)7–8(–8·5) μm.

The even distribution of the ascomata suggests that this species is lichenized, but the possibility that it may be a lichenicolous fungus on an unidentified host cannot be conclusively eliminated in the absence of further fresher material; at least the species must be a parasymbiont. This species is clearly closely allied to *Polycoccum* Sauter ex Körber, but the wall structure is not typical for that genus which characteristically has walls which are pseudoparenchymatous (textura angularis) throughout. The absence of a distinct clypeus and also the tendency of the walls to be pseudoparenchymatous near the ostiole means that the species cannot be readily placed in *Clypeococcum* D. Hawksw. For the time being it seems most appropriate to place this species in *Polycoccum* and the combination **Polycoccum innatum** (Müll. Arg.) D. Hawksw., **comb. nov.**, is therefore made here.

Microthelia inops Degel. in *Ark. Bot.* **30** (3): 16 (1942).

The holotype and other material in herb. Degelius was studied by Hawksworth (1985*a*) who concluded that the species was a later synonym of *Kirschsteiniothelia aethiops* (Berk. & Curtis) D. Hawksw.

Microthelia leightonii Zahlbr., *Cat. Lich. Univ.* **1**: 260 (1921).

Type: British Isles, South Devon, Torquay, on limestone, *R. Deakin* (K—holotype).

Verrucaria leightonii Deakin in *Ann. Mag. nat. Hist.* II, **13**: 34 (1854), nom. illegit. (Art. 64.1), non *V. leightonii* Hepp, *Flecht. Eur.* exs. 95 (1853).

The epithet in *Microthelia* correctly dates from 1921 and should be attributed to Zahlbruckner alone in accordance with Art. 72 note 1.

Examination of the holotype established that this name should be placed as a further synonym of *Rinodina bischoffii* (Hepp) Massal. (Mayrhofer & Poelt, 1979: 62–63); *R. bischoffii* still occurs in the vicinity (Hawksworth, 1973: 62).

There is also a specimen ex-herb. Piggott in BM labelled '*Verrucaria leightonii* Deakin', but not in Deakin's hand, from Torquay which could be an isotype; likewise this belongs to *R. bischoffii*.

Microthelia linderi Kohlm. in *Trans. Br. mycol. Soc.* **57**: 483 (1971).

A new name introduced for *Microthelia maritima* (Linder) Kohlm. non B. de Lesd. and automatically typified by the holotype of *Amphisphaeria maritima* Linder which was referred to the genus *Kirschsteiniothelia* by Hawksworth (1985*a*).

Verrucaria lyellii Leighton, *Br. Sp. Angiocarp. Lich.*: 45 (1851).

Type: British Isles, Hampshire, New Forest, *C. Lyell* (K-Borr.—holotype).

Leiophloea lyellii (Leighton) Trevisan, *Consp. Verruc.*: 8 (1860).

This name was listed as a synonym of *Microthelia micula* by both Zahlbruckner (1921: 262) and Müller & von Arx (1962: 284). Examination of the holotype showed that the ascospores were pale brown, 3-septate, and 15–17 × 3·5–5 μm when mature. The fungus falls within the range of variation exhibited by *Melanomma pulvis-pyrius* (Pers.) Fuckel, and Leighton's epithet should be treated as a later synonym of that species. The ascomata are erumpent through the thallus of *Graphis scripta* (L.) Ach. in the holotype, but originate from the bark; this is not a lichenicolous fungus.

Kirschsteiniella macedonica Petrak in *Annls mycol.* **34**: 213 (1936).

Type: Greece, Macedonia, Schlucht von Demirkapu, on *Ephedra major*, 8 February 1931, *A. Ade* (W 1978/11832—holotype).

Examination of the holotype established that this name was a later synonym of the ubiquitous *Didymosphaeria futilis* (Berk. & Broome) Rehm; the ascomata are entirely immersed and rather large (to 500 μm wide in vertical section) but fall within the range of variation of the species as interpreted by Scheinpflug (1958). I cannot understand why Petrak referred this fungus to *Kirschsteiniella*.

Microthelia macquariensis Dodge in *Rep. B.A.N.Z. antarctic Res. Exped.* B, **7**: 48 (1948).

This species, described from Macquarie Island, was stated to form circular thalli about 0·2 mm diam and to have entire perithecia to 0·1 mm diam, evanescent paraphyses, and 1-septate ascospores 15 × 4 μm. In view of the small size of the thalli and lack of persistent paraphyses there can be little doubt that this represents a species of *Endococcus* close to, if not identical with, the widespread *E. rugulosus* Nyl.

Microthelia macrocarpoides Zahlbr. in *Ann. cryptog. Exot.* **5**: 199 (1932).

Type: South Africa, Knysna, Die Hoofde, on *Olea* sp. bark, January 1928, *P. A. van der Byl* 661 (W 1928/13950—holotype).

Fig. 64A–F.

This taxon has massive black hemispherical ascomata (400–)500–700(–900) μm diam. The ascomatal wall is pseudostromatic, including some host tissue to form a clypeus, but within that is a pseudoparenchymatous exciple lining the ascomatal cavity, which is applanate at the base. The paraphyses are abundant, persistent, very sparsely branched and 2–3·5 μm wide; the hymenial gelatin turns blue with iodine. Of especial interest are the asci which are rather thick-walled, but have a canal extending into the apex which is

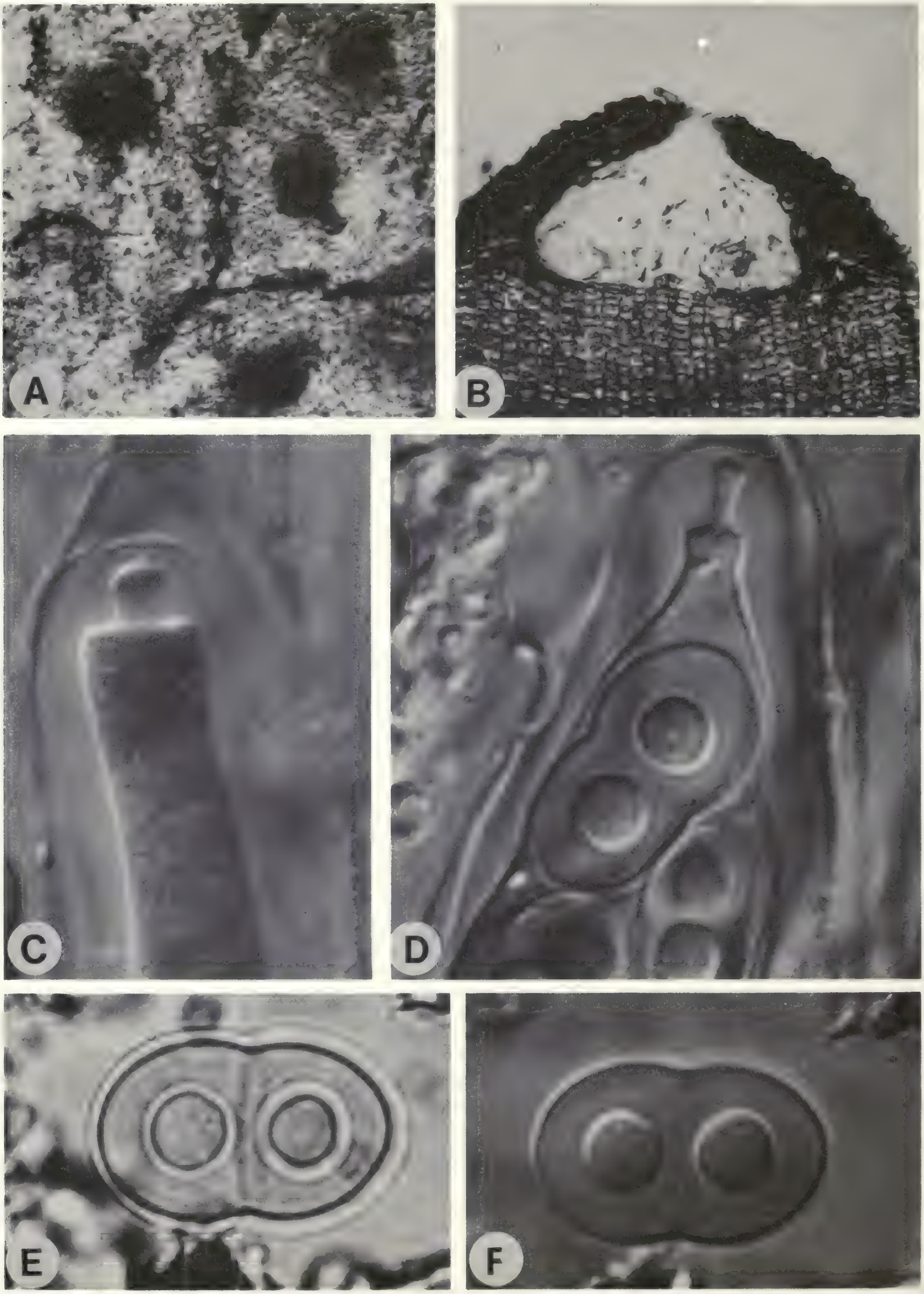

Fig. 64 *Microthelia macrocarpoides* (W 1928/13950—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 100. **C**, Ascus tip in differential interference contrast showing refractive annulus (pair of dots in optical section) above the internal apical beak, × 2500. **D**, Ascus tip in an older ascus showing the cruciform internal apical beak in differential interference contrast, × 2500. **E**, Ascospore as seen by normal light microscopy, × 2500. **F**, Ascospore as in E as seen by differential interference contrast, × 2500.

rather swollen and cruciform; in young asci, above the swollen upper chamber, an annulus was demonstrated several times. The ascospores have exceptionally thick walls, developing a single septum late, a somewhat wrinkled to verruculose outer surface, and are subhyaline to pale golden brown measuring 15·5–20 × 7·5–11 μm. The fungus is almost certainly congeneric with *Verrucaria hymenothora* and *Microthelia aurora* (see p. 150), but the ascomata are not as immersed. According to Zahlbruckner (loc. cit.) the species had *Trentepohlia* as a photobiont.

Verrucaria magnospora Knight in *Trans. Linn. Soc. Lond.* **23**: 99 (1860).

Type: New Zealand, [sine loc.] *C. Knight* (WELT—holotype; G—isotype).

Verrucaria magnifica Nyl., *Lich. Nov. Zel.*: 132 (1888), nom. illegit. (Art. 63.1).
Microthelia magnifica (Nyl.) Müll. Arg. in *Bull. Soc. r. bot. Belg.* **31**: 41 (1892), nom. illegit. (Art. 63.1).

Illustrations: Knight in *Trans. Linn. Soc. Lond.* **23**: tab. 11 fig. 5 (1860).—Nylander, *Lich. Nov. Zel.*: tab. 1 fig. 5 (1888).

Examination of the holotype and isotype established that this name refers to a melanommataceous lichenized species with massive dimidiate ascomata 300–500(–700) μm diam, 8-spored, elongate-clavate bitunicate asci, about 75 × 23 μm, branched and anastomosing delicate paraphysoids about 1 μm thick, and distichously arranged ascospores which are essentially hyaline (rarely becoming slightly fuscous brown after discharge), 1-septate, constricted at the septum, almost equal-celled, very thick-walled, smooth-walled, and 40–56 × 17–22 μm (in those seen by me; the range reported in the literature is 36–50 × 18–27 μm).

Even though the ascospore septum is more or less central, this species is most appropriately referred to *Anisomeridium* (Müll. Arg.) M. Choisy and the combination *A. magnosporum* (Knight) D. Hawksw. has been made to accommodate this species (*in* Galloway, 1983: 195) *A. magnosporum* recalls an undescribed species from Florida which differs in having rather narrower ascospores (12–20 μm wide), conspicuously eccentric ostioles, and an orange pigment around the ostiole which turns purple in potassium hydroxide (Harris, 1975: 112).

The specimen in G cited above is labelled 'Dr. Knight. 1883' in Müller's hand and has an older label glued to it written by Knight; in listing this as an isotype I am assuming Knight sent this fragment to Müller in 1883.

Microthelia maritima B. de Lesd., *Rech. Lich. Dunkerque*: 254 (1910).

This species was described from a piece of bamboo placed between some stones at Dunkirk, France, which was covered by the sea at high tide. According to the original description, the perithecia arose on a brownish crust, were 100–200 μm broad, hemispherical, with branched and anastomosing paraphyses; the asci were cylindrical, 8-spored, and the ascospores 1-septate and 19–26 × 6–7 μm. As Bouly de Lesdain's early herbarium was destroyed in 1940 (Laundon, 1979: 7), the application of this name must remain uncertain.

Amphisphaeria maritima Linder in *Farlowia* **1**: 411 (1944).

Microthelia maritima (Linder) Kohlm. in *Nova Hedwigia* **2**: 322 (1962), nom. illegit. (Art. 64.1), non *M. maritima* B. de Lesd., *Rech. lich. Dunkerque*: 254 (1910).

The holotype of this species was studied by Hawksworth (1985*a*: 193) who found that the fungus was most appropriately called *Kirschsteiniothelia maritima* (Linder) D. Hawksw.

Tichothecium marmoratum Krempelh. in *Denkschr. K. bayer. bot. Ges. Regensb.* **4**: 298 (1861).

Microthelia marmorata (Krempelh.) Hepp *in* Körber, *Parerg. Lich.*: 398 (1865).
Mycoporum marmoratum (Krempelh.) Nyl. *in* Stizenberger in *Ber. Tät. St. Gall. naturw. Ges.* **22**: 515 (1882), as 'Nyl. in *lit.*'.

This fungus appears to be primarily lichenicolous on various pyrenocarpous lichens on calcareous rocks, but sometimes appears to become facultatively lichenized taking over *Trentepohlia* from its original host. The structure of the entire perithecioid ascomata and the brown and warted 1-septate ascospores are characteristic of *Polycoccum*, to which genus the species was transferred as *P. marmoratum* (Krempelh.) D. Hawksw. (*in* Hawksworth et al., 1980: 107). A description and illustration is provided by Swinscow (1966: 234–235).

Microthelia melanostigma Th. Fr. in *J. Linn. Soc.* (Bot.) **17**: 368 (1879).

This species was described on the basis of material 'On stones in the vicinity of Floeberg Beach' collected at 82°26′30″N by Captain Feilden on a Polar Expedition. The material was sent by J. D. Hooker to Th. Fries but could not be located in UPS (R. Moberg, in litt.) nor in BM. The ascomata were given as 100–200 μm diam and the blackish brown spores measured 10–14 × 5–7 μm. As Th. Fries described the paraphyses as 'nullae distinctae' it is possible that he was dealing with a *Muellerella* species but this must remain uncertain in the absence of original material. The name does not appear to have been taken up by any subsequent author.

Amphisphaeria melantera J. B. Ellis & Everh. in *Bull. Torrey bot. Club* **24**: 278 (1897).

Type: U.S.A., Colorado, Deansbury, on *Quercus undulata* bark, April 1897, *E. Bethel 230* (NY—holotype).

Splanchnonema melanterum (J. B. Ellis & Everh.) Barr in *Mycotaxon* **15**: 354 (1982).

This fungus was placed by Sivanesan (1976: 398) as a synonym of the species now named *Kirschsteiniothelia aethiops* (Hawksworth, 1985*a*). The ascospores of *Amphisphaeria melantera* are exceptionally thick-walled and measure 34–40 × 13·5–15·5 μm, too large for *K. aethiops*. Furthermore, the ascospores are smooth-walled at maturity, almost equal-celled, and with smoothly rounded apices. The species clearly has nothing to do with *K. aethiops* and was transferred to *Splanchnonema* Corda (Pleomassariaceae) by Barr (1982).

Verrucaria melasperma Nyl. in *Flora, Jena* **48**: 357 (1865).

Microthelia melasperma (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 289 (1903).
Phaeosporis melasperma (Nyl.) Clem., *Gen. Fungi*: 173 (1909).

This species was originally described 'supra terram prope Brest' from a collection of the brothers Crouan and stated to produce simple brown ascospores 14 × 7 μm uniseriately arranged in the asci. The type material was studied by Vainio (1921*b*: 26) who merely reported it as 'sec. specim. orig. est Fungus'. The fungus is clearly nothing to do with the other genera accepted in this paper and its correct position is uncertain. Before introducing the new generic name *Phaeosporis* Clem. for this species, it seems unlikely that Clements ever saw material of Nylander's taxon, but at least it may provide a temporary position pending re-examination of the type.

Microthelia membranacea Anzi in *Atti Soc. ital. Sci. nat.* **9**: 256 (1866).

Type: Italy, 'Lanzada in Val Malenco', on *Cytisus laburnum, M. Anzi* (not traced).

This species was described as forming ± spherical ascomata, immersed at the base, which produced 6-spored (!) asci and brown 1-septate ascospores 24 × 8·6 μm. The ascospore dimensions led Keissler (1936: 30) to consider the name as a possible synonym of the species now called *Peridiothelia grandiuscula*, but in the absence of material the name is better treated as of uncertain application, at least while similar material on *Cytisus* is unknown. Anzi's main herbarium is in TO but no reply was received to requests for this material.

Microthelia metzleri Lahm *in* Körber, *Parerg. Lich.*: 398 (1865).

Holotype and isotype material was investigated by Hawksworth (1981*b*: 143) who found it to be a valid species of *Lichenothelia* called *L. metzleri* (Lahm) D. Hawksw.

Microthelia microsperma Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **32**: 171 (1894 ['1893']).

Type: Costa Rica, 'Forêt du Rio Général', 1893, *H. Pittier* [6305] (G—holotype).

Fig. 65A–C.

This taxon has massive pseudostromatic ascomata which are black, radially striate, and 500–800 μm diam. The clypeate stromatal tissue, involving host cells, entirely surrounds the generative locule which is further enclosed in a complete exciple which is hyphal in structure. The hamathecium is well-developed, and composed of paraphysoids which are, filiform, branched, and mainly about 1 μm thick. The subcylindrical 8-spored asci, 30–37 × 5 μm, have monostichously overlapping to somewhat distichously arranged ascospores. The ascospores themselves are ellipsoid, 1-septate, slightly or not constricted at the central septum, the cells equal in size with rounded apices, golden brown, smooth-walled, without a conspicuous sheath, and only 5–7 × 2–3 μm. Evidently not lichenized.

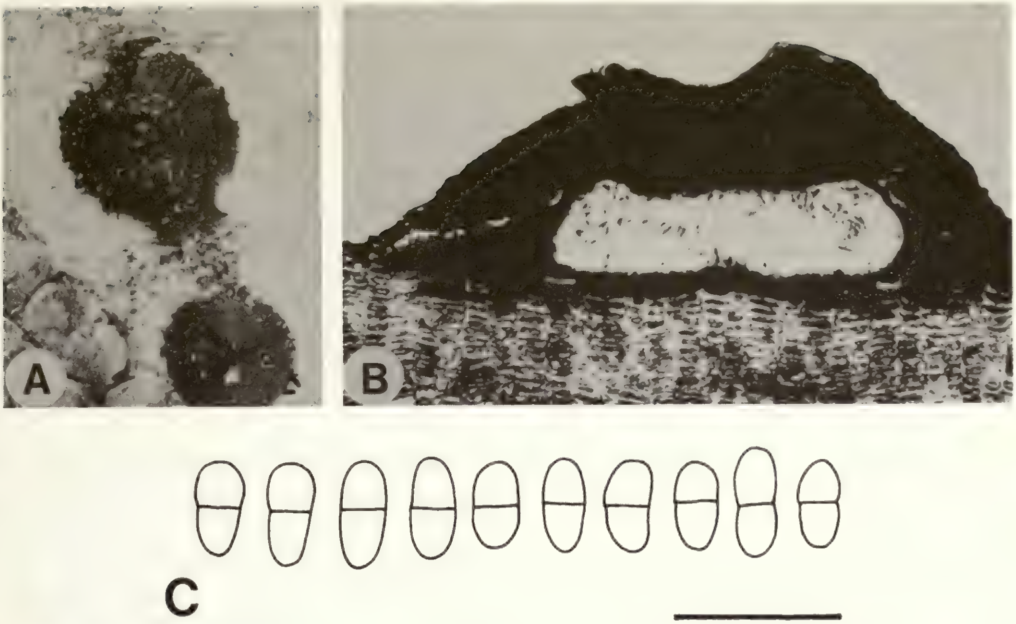

Fig. 65 *Microthelia microsperma* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section, × 100. **C**, Ascospore outlines, scale = 10 μm.

Microthelia microsperma is possibly related to *Didymosphaeria futilis*, but is distinguished by the massive pseudostromatic tissue and smaller ascospores. Whether the stroma is sufficient for segregation at the generic level is unclear at the present time pending further studies on *Didymosphaeria* s. lat., but it seems possible that a new generic name may eventually have to be introduced for this species.

Microthelia micula Flotow ex Körber, *Syst. Lich. Germ.*: 373 (1855), nom. illegit. (Art. 63.1).

Verrucaria micula (Flotow ex Körber) Garov., *Tent. Disp. Lich. Langob.*: 79 (1865).
Verrucaria cinerella f. *micula* (Flotow ex Körber) Nyl. *in* Ohlert in *Schr. phys.-ökon. Ges. Königsb.* **11**: 42 (1870), as '(Nyl. in litt.)'.
Didymosphaeria micula (Flotow ex Körber) Rehm *in* Saccardo, *Syll. Fung.* **1**: 715 (1882).
Mycomicrothelia micula (Flotow ex Körber) V. Wirth, *Flechtenfl.*: 348 (1980), comb. inval. (Arts 33.1, 34.1).

In the discussion following the introduction of this epithet Körber (loc. cit.) stated:

> 'Ich ehe nichts "Zweigestaltiges" an dieser Flechte, weshalb ich den (ohnediess anderweitig vielfach gebrauchten) Borrer'schen Speciesnamen *"biformis"* nicht annahm.'*

It is therefore clear that Körber intended to introduce a new name as a substitute for *Verrucaria biformis* Borrer which he considered to be inappropriate. As a result, Körber's epithet is superfluous and therefore illegitimate (Art. 63.1) and automatically typified by the type of Borrer's name (Art. 7.11); i.e. it becomes an obligate synonym of the species now known as *Anisomeridium biforme* (see p. 138).

Körber misinterpreted Borrer's species, describing the spores as 'fuscae'. He also cited two exsiccatae (Hepp, *Flecht. Eur.* 108; Zwackh, *Lich. exs.* 110) and specimens collected by himself, Arnold and Flotow. Of these collections, only that made by Arnold is now present in L (Nymphenburg, on *Tilia*, May 1854, *F. G. C. Arnold*, L 910.195-388) and this belongs to the species called *Peridiothelia fuliguncta* in this revision (p. 121). Körber (1865: 397) mentioned a third exsiccatum as belonging to *M. micula*, Schaerer's *Lich. exs.* 109, which also belongs to *P. fuliguncta* and includes a piece of bark with *Acrocordia gemmata* (Ach.) Massal., a species similar in many respects to *Anisomeridium biforme*. Five other packets are under this name in Körber's herbarium; four of these represent *P. fuliguncta* and the fifth a fungus on lignum belonging to *Didymosphaeria* s. lat.

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* *Translation:* 'I do not see anything dimorphic in this lichen, that is why I did not accept Borrer's species name *"biformis"* (already used frequently elsewhere).'

Microthelia minor Kernst. in *Verh. zool.-bot. Ges. Wien* **46**: 307 (1896).

Type: Austria, Tirol, Penedal, *E. Kernstock* (W 1900-4389—lectotype).

Microthelia marmorata f. *minor* (Kernst.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 45 (1936).

Two localities were mentioned in the original description, Marocche and Penedal; only material from the latter site was sent for study from W and, as this collection was also studied by Keissler, it is designated as the lectotype. Numerous lichens are present on the limestone sample supporting the species, which is most probably lichenicolous. Rather few ascomata remain but these are erumpent, subglobose, black, 100–200 μm diam, the peridium is textura angularis, and the ascospores are dark brown, 1-septate, distinctly verruculose, and measure (12–)13–16(–18) × 7–10(–11) μm. No intact asci were found in the few ascomata squashed and the nature of the interascal tissue could not be conclusively determined; the hymenial gelatine reacted blue with iodine (Keissler, loc. cit., stated that it turned red). This fungus is most probably a species of *Polycoccum* Sauter ex Körber and may be distinct; *P. microstictum* (Leighton) Arnold has rather similarly sized ascospores but they have a different shape (higher length : breadth ratio). In the absence of material with intact asci in which the interascal tissues could be studied it would be premature to make a new combination for Kernstock's fungus.

Microthelia nephromaria Lindsay in *Trans. R. Soc. Edinb.* **25**: 539 (1869), nom. illegit. (Art. 63.1).

Sphaerulina nephromaria (Lindsay) Vouaux in *Bull. Soc. mycol. Fr.* **29**: 34 (1913), nom. illegit. (Art. 63.1).

In introducing this epithet, Lindsay (loc. cit.) considered this taxon to be conspecific with *Lecidea alectoriae* Lindsay, a previously published name (Lindsay, 1859: 135), stating '. . . I merge the two in a single type, and abolish both the generic and specific designations as inappropriate'; the name *Microthelia nephromaria* is consequently superfluous and must be rejected under Art. 63.1 and automatically typified by the nomenclatural type of *Lecidea alectoriae* in accordance with Art. 7.11. This latter epithet was based on a fungus on a *Neuropogon* species collected in Kerguelen's Land during J. D. Hooker's antarctic voyage of 1839–43; study of the holotype (E) established that it produced hyaline ascospores *c.* 14 × 3·5 μm with a single septum but enclosed in an epispore; the ascomata appear to be aparaphysate, immersed, *c.* 125 μm wide, with a peridium composed of pseudoparenchymatous cells. The generic position of this fungus is currently unclear but it is obviously unrelated to other taxa accepted in the present revision.

Microthelia dispora f. **octospora** W. Watson in *J. Bot., Lond.* **63**: 123 (1925).

Type: British Isles, Gloucestershire, Crickley Hill, on oolitic stones on the ground, 26 March 1923, *H. H. Knight* (K—holotype).

Examination of the holotype confirmed the determination of Swinscow (1966: 235), based on an isotype in NMW, that this taxon is a synonym of the species now called *Polycoccum marmoratum* (Hepp) D. Hawksw. (see p. 155).

Microthelia oxyspora Zahlbr. in *Annls mycol.* **33**: 36 (1935).

Type: U.S.A., Florida, Sanford, on *Quercus*, *J. Rapp* 73 (W 1934/330—holotype).

Fig. 66.

In vertical section the ascomata were found to be entire and to be immersed in the bark at the base; they are subglobose, mainly 150–200 μm diam, with dark brown walls to *c.* 60 μm thick. The paraphysoids are trabeculate, branched and anastomosing, and 1–1·5 μm thick and the ascospores are red-brown, broadly

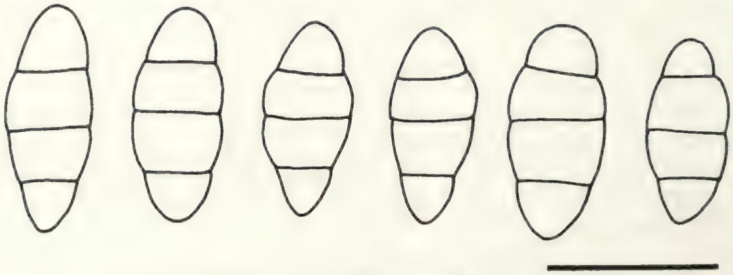


Fig. 66 *Microthelia oxyspora* (W 1934/330—holotype) ascospore outlines. Scale = 10 μm.

fusiform, smooth, 3-septate, and (11–)12–14 × (4–)5–6·5 μm in size. This species consequently belongs to *Melanomma* Nitschke ex Fuckel, but does not agree with any of the species treated by Holm (1957). The North American species of this genus are in need of revision but, since this material does not agree with any currently accepted, the new combination **Melanomma oxysporum** (Zahlbr.) D. Hawksw., **comb. nov.**, is made here. Although the bases of the ascomata are seated in the bark, they are erumpent through a whitish trentepohlioid crust so could conceivably be at least partly lichenized.

Microthelia palavana Vainio in *Annls Acad. Sci. fenn.* A, **15** (6): 347 (1921).

Type: Philippine Islands, Palawan, Taytay, April 1913, *E. D. Merrill* 9036 (BM—isotype).

Contrary to the original description of the species, the ascospores remain hyaline when mature and measure 17–24 × 7–11 μm. The uniseriate arrangement of the ascospores and the filamentous paraphysoids indicate that this species belongs to *Acrocordia* Massal. It is rather close to *A. gemmata* (Ach.) Massal., but the spore shape differs slightly. As the tropical species of *Acrocordia* are so imperfectly known it would be premature to transfer Vainio's epithet to that genus because another earlier name may be available.

Microthelia anthracina f. **pallidior** Kernst. in *Verh. zool.-bot. Ges. Wien* **40**: 324 (1890).

Type: Austria, Tirol, Thouschiefes, Piuyolo, *E. Kernstock* (W 1900/4392—holotype).

Microthelia aterrima f. *pallidior* (Kernst.) Zahlbr., *Cat. Lich. Univ.* **1**: 256 (1921).
Microthelia metzleri var. *pallidior* (Kernst.) Migula, *Fl. Deutschl.* II, **12** (2): 563 (1930).

This name was treated as a synonym of *M. aterrima* by Keissler (1936: 40) but examination of the presumed holotype (no specimen was detailed by Kernstock, loc. cit. but that cited above is labelled 'f. *pallidior* m') showed that it was typical material of *Phaeospora parasitica* (Lönnr.) Arnold growing on a sterile whitish crustose thallus, most probably a *Rhizocarpon*.

Mycomicrothelia palmarum Chaudhury & P. Rao in *Mycopathologia* **22**: 220 (1964).

The description, illusrations, and measurements given in the original account of this species, described from living leaves of *Cocos nucifera* in Hyderabad, India, agree so closely with those of *Didymosphaeria futilis* (Berk. & Broome) Rehm that there can be little doubt that *Mycomicrothelia palmarum* is a further synonym of this omnivorous species.

Microthelia parietinaria Lindsay in *Trans. R. Soc. Edinb.* **25**: 541 (1869).

Type: British Isles, Norfolk, Coltishall ['Cottishall'], on *Xanthoria parietina, D. Turner* (BM—holotype).

Didymosphaeria parietinaria (Lindsay) Sacc., *Syll. Fung.* **17**: 681 (1905).
Endococcus parietinarius (Lindsay) Clauzade & Roux, *Champ. Lich. Non-Lich.*: 28 (1976).

No type material was located in BM, E, or K by Hawksworth (1982), but what is undoubtably the holotype has now been found in BM filed under *Lecanora populicola*. The material is not annotated by Lindsay but it is from K stamped 'Herbarium Hookerianum 1867'. This agrees with material forming galls on *Xanthoria parietina* collected in Somerset in 1981, described by Hawksworth (1982; as '*Endococcus parietinus*'). The species has since been re-collected in Somerset (Wedmore, Stoke Moor, January 1983, *E. McDonnell*, IMI 277766) and also seen from Scotland (Balnakiel churchyard, 1978, *C. J. B. Hitch*, hb Hitch).

Verrucaria peripherica Taylor *in* MacKay, *Fl. Hib.* **2**: 97 (1836).

Microthelia peripherica (Taylor) Mudd, *Man. Br. Lich.*: 308 (1861).

The holotype was examined by Hawksworth (1979*b*: 555) and found to be a species of *Pleospora* (subgen. *Montagnula*), *P. peripherica* (Taylor) D. Hawksw.; a description and illustration of the ascospores were provided.

Microthelia perrugosaria Lindsay in *Trans. R. Soc. Edinb.* **24**: 437 (1866).

Type: New Zealand, Otago, Kaikorau Hill, on *Placopsis perrugosaria* (Nyl.) Nyl. (apothecia), *W. L. Lindsay* (not traced).

Didymosphaeria perrugosaria (Lindsay) Sacc. & Trotter *in* Saccardo, *Syll. Fung.* **22**: 176 (1913).

The type material of this species could not be located in E (B. J. Coppins, in litt.). The fungus was described and illustrated in such detail by Lindsay that there can be little doubt that it represents a species of *Polycoccum*. Several fungi probably referrable to this genus have been described from *Placopsis* species (Lamb, 1947: 177–178) but their taxonomy has not been revised in recent years. It is possible that Lindsay's name is an additional synonym of *Polycoccum squamarioides* (Mudd) Arnold which occurs on the thallus of *Placopsis gelida* (L.) Lindsay (see Zopf, 1897: 113–117), but the ascospores appear to be slightly shorter than is usual for that species.

Microthelia petraeicola Lindsay in *Q. Jl microsc. Sci.* II, **11**: 41 (1871).

Type: Switzerland, Buembach, on *Rhizocarpon obscuratum* (Ach.) Massal., *L. E. Schaerer* [*Lich. Exs.* 183; sub *Lecidea petraea* Ach.] (E—holotype).

Examination of the holotype confirmed that this name was a synonym of the lichenicolous fungus *Phaeospora parasitica* (Lönnr.) Arnold as stated by Keissler (1930: 423). The ascospores are 3-septate, brown when mature, constricted at the septa, and 14–15 × 6–7 μm in Schaerer's material.

Microthelia pharaonis Müll. Arg. in *Revue mycol.* **2**: 81 (1880).

Verrucaria pharaonis (Müll. Arg.) Stizenb. in *Ber. Tät. St. Gall. naturw. Ges.* **1889/90**: 217 (1891).

This taxon was described as lacking paraphyses and differing from *Tichothecium pygmaeum* (see below) mainly in that the asci were not multispored. As the ascospores were stated to be 9–11 × 4–4·5 μm, this name is probably synonymous with *Endococcus propinquus* (see below).

Microthelia ploseliana B. Stein *in* Cohn, *Krypt.-Fl. Schles.* **2** (2): 331 (1879).

The original material on which this species was based was examined by Keissler (1936: 55) who reported that it was identical with the lichenicolous fungus '*Discothecium gemmiferum* (Taylor) Vouaux'; the ascospore dimensions of 8–11 × 5–6 μm indicate that this is almost certainly the species now called *Endococcus propinquus* (Körber) D. Hawksw. (see Hawksworth, 1979*a*: 287).

Microthelia propinqua Körber, *Syst. Lich. Germ.*: 374 (1855).

This epithet was neotypified and taken up by Hawksworth (1979*a*: 287) for the common lichenicolous fungus previously called *Tichothecium gemmiferum* auct. [non (Taylor) Körber] in the combination *Endococcus propinquus* (Körber) D. Hawksw.

Microthelia prunastria Lindsay in *Q. Jl microsc. Sci.* II, **9**: 349 (1869), as '*prunastri*', nom. inval. (Art. 32.1).

Microthelia prunastraria Arnold in *Flora, Jena* **57**: 155 (1874), [?lapsus], nom. inval. (Art. 32.1), nom. illegit. (Art. 63.1.).

Lindsay (loc. cit.) refers to a note by Körber (1855: 43) which, in a discussion of *Evernia prunastri* (L.) Ach., merely states 'Oft ist auch das Lager mit schwarzen punktförmigen Wärzchen, die zum Theil Spermogonien, zum Theil parasitische Pilzbildungen sind, reichlich besetzt.' This cannot be considered as a description or diagnosis in the sense of Art. 32 so both Lindsay's and Arnold's epithets must be treated as not validly published; neither has been taken up by subsequent authors. It is possible Körber was dealing with *Lichenoconium erodens* M. S. Christ. & D. Hawksw. as that species frequently forms black pycnidia on this host (Hawksworth, 1977: 175–176), but several other lichenicolous fungi are also now known from *E. prunastri*.

Microthelia puyae Speg. in *Revta Fac. Agron. Vet. Univ. La Plata*, II, **6**: 71 (1910).

Didymosphaeria puyae (Speg.) Sacc. & Trotter *in* Saccardo, *Syll. Fung.* **22**: 176 (1913).

The original illustration published by Spegazzini (loc. cit.: 72) shows the ascomata to be *completely* immersed in the decaying leaves of the host (*Puya chilensis*) with only the ostiolar region deeply pigmented and slightly extended into an involucrellum; the paraphyses were figured as simple and the 8-spored asci as thin at the apex. The ascospores were sheathed and stated to measure 20–22 × 9–10 μm. If the fungus was bitunicate, the species could probably be more appropriately accommodated in the current broad concept of *Venturia* de Not. (Sivanesan, 1977).

Tichothecium pygmaeum Körber in *Denkschr. Schles. Gesell. vat. Cult.* **1853**: 236 (1853).

Microthelia pygmaea (Körber) Körber, *Syst. Lich. Germ.*: 374 (1855).

For further synonyms see Keissler (1930: 411–412) and for typification see Santesson (1960: 506). This species was re-investigated by Hawksworth (1979*a*: 289), who found that it was most appropriately referred to *Muellerella* Hepp ex Müll. Arg., and made the combination *M. pygmaea* (Körber) D. Hawksw.

Pyrenula cinerella var. **quadriloculata** Fink in *Minn. bot. Stud.* **2**: 276 (1899).

Pyrenula cinerella subsp. *quadriloculata* (Fink) Fink in *Contr. U.S. natn. Herb.* **14**: 239 (1910).
Microthelia micula var. *quadriloculata* (Fink) Zahlbr., *Cat. Lich. Univ.* **1**: 263 (1921).

The holotype of this taxon in MICH was studied by Harris (1973: 49–50) who found it to comprise *Polyblastiopsis falliciosa* (Stizenb. ex Arnold) Zahlbr. intermixed with an unrelated coelomycete producing brown 3(–4) septate conidia which also occasionally had an additional longitudinal septum. The name is correctly typified by the coelomycete element, as it was this which provided the diagnostic features of the taxon; Fink at first gave the spores as 12–15 × 5–6·5 μm but later as 10–18 μm long (Fink, 1910: 239).

Microthelia queenslandica Müll. Arg. in *Rept. Austral. Soc. Advmt Sci.* **6**: 455 (1895).

Type: Australia, Queensland, 1887, *C. Knight* 71 (G—lectotype).

Fig. 67A–D.

In the original description several collections made by Knight in Queensland were cited: 'n. 5, 29, 56 et plures alii'. In G collections numbered 5, 56 = 71, 56a (these three stuck on one piece of paper), 70, 71 (71 = 56) (these two in a single packet) as well as three further packets are preserved. These prove to be a mixture of (a) *Mycomicrothelia obovata*, which predominates, and (b) a melanommataceous fungus with a hamathecium of paraphysoids 1–1·5 μm wide producing symmetrical 3-septate (sometimes with to two additional incomplete septa) ascospores which are olivaceous brown, distinctly verruculose, the walls internally thickened and tending to become distoseptate with the septae towards the apices, a conspicuous gelatinous sheath to 4 μm thick in potassium hydroxide, and measure 32–42 × 11–14 μm (40–48 × 14–17 μm according to the original description!). The latter fungus evidently provided the diagnostic characters of the taxon as further evidenced by specimen 71 being annotated in Müller's hand 'plures alii' but omitted as equivalent to 56 from the original description. The generic placement of specimen 71 is unclear. The fungus may well be referrable to either the Pyrenulaceae or to the Massariaceae, although it cannot be satisfactorily accommodated in any of the genera treated in the latter by Barr (1979*b*). This species needs to be considered in a future treatment of the tropical Pyrenulales.

Microthelia ramalinaria Lindsay in *Trans. R. Soc. Edinb.* **24**: 440 (1866).

This species was lectotypified by Hawksworth (1976: 54) and is currently accepted as *Endococcus ramalinarius* (Lindsay) D. Hawksw. (Hawksworth, 1979*a*: 287).

Verrucaria conformis f. **rhypontoides** Nyl. *in* Leighton, *Lich. Fl. Gr. Br.*: 430 (1871).

Type: British Isles, Channel Islands, Jersey, Noirmont, 1868, *C. du Bois Larbalestier* (H-NYL 861—holotype).

Arthopyrenia conformis f. *rhypontoides* (Nyl.) Zahlbr., *Cat. Lich. Univ.* **1**: 321 (1921).
Microthelia rhypontoides (Nyl.) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 29 (1936).

The type material is now in poor condition and comprises a few black pycnidia on wood. Keissler (1936: 29) studied this material, and reported finding brown 1-septate spores identical to those of *Microthelia fuliguncta* Norman (see p. 121). The name must now be regarded as of uncertain application. If Keissler's interpretation was correct, Norman's epithet should have been employed because it has priority at the rank of species (Art. 60).

Verrucaria ribesiella Nyl. ex Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 195 (1883), as 'Nyl. in sched. 1877'.

Type: U.S.S.R., Karelia australis, Viborg, 'Monrepos', on *Ribes grossularia*, 1875, *E. A. Vainio* (H-NYL 858—lectotype).

Didymosphaeria ribesiella (Nyl. ex Vainio) Vainio in *Acta Soc. Fauna Fl. fenn.* **49** (2): 149 (1921).
Microthelia ribesiella (Nyl. ex Vainio) Zahlbr., *Cat. Lich. Univ.* **8**: 79 (1931).
Microthelia macularis f. *ribesiella* (Nyl. ex Vainio) Keissler, *Rabenh. Krypt-Fl.* **9**, 1 (2): 37 (1936).
Mycomicrothelia macularis f. *ribesiella* (Nyl. ex Vainio) Keissler, *Rabenh. Krypt.-Fl.* **9**, 1 (2): 36 (1936).

Fig. 68A–B.

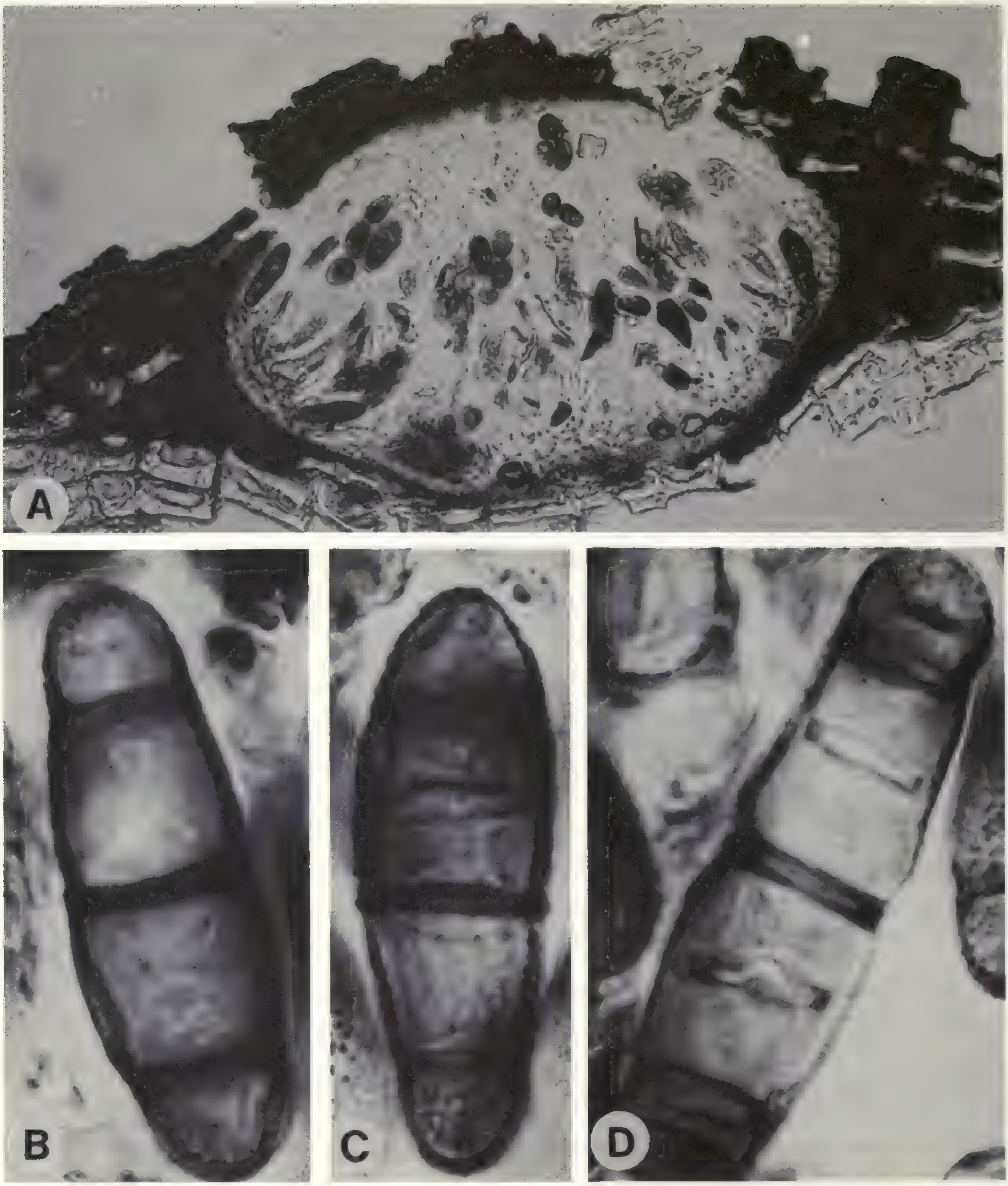


Fig. 67 *Microthelia queenslandica* (*Knight* 5, G—syntype). **A**, Vertical section of ascoma, × 250. **B–D**, Ascospores, × 2200.

Two collections were mentioned in the first published description of this species; that designated as lectotype above and another (Finland, Karelia borealis, Nurmes, on *Ribes grossularia*, 1875, *E. A. Vainio*, H). These specimens agree in all details and the one from Viborg is selected as the lectotype because that was definitely seen by Nylander while that from Nurmes may not have been.

The ascomata are completely immersed in the host twigs, to *c.* 180 μm diam, only the tip of the ostiole protruding, subglobose, lacking an involucrellum, the walls pseudoparenchymatous, composed of brown (to subhyaline below) angular cells, somewhat thicker in the vicinity of the ostiole. The pseudoparaphyses are abundant, cellular, branched and anastomosing, *c.* 3 μm thick, and the asci elongate-clavate, bitunicate with 8 distichously arranged ascospores. The ascospores themselves are broadly fusiform, attenuated at the apices, 1-septate at first but becoming 3-septate when mature, constricted at the central septum, pale

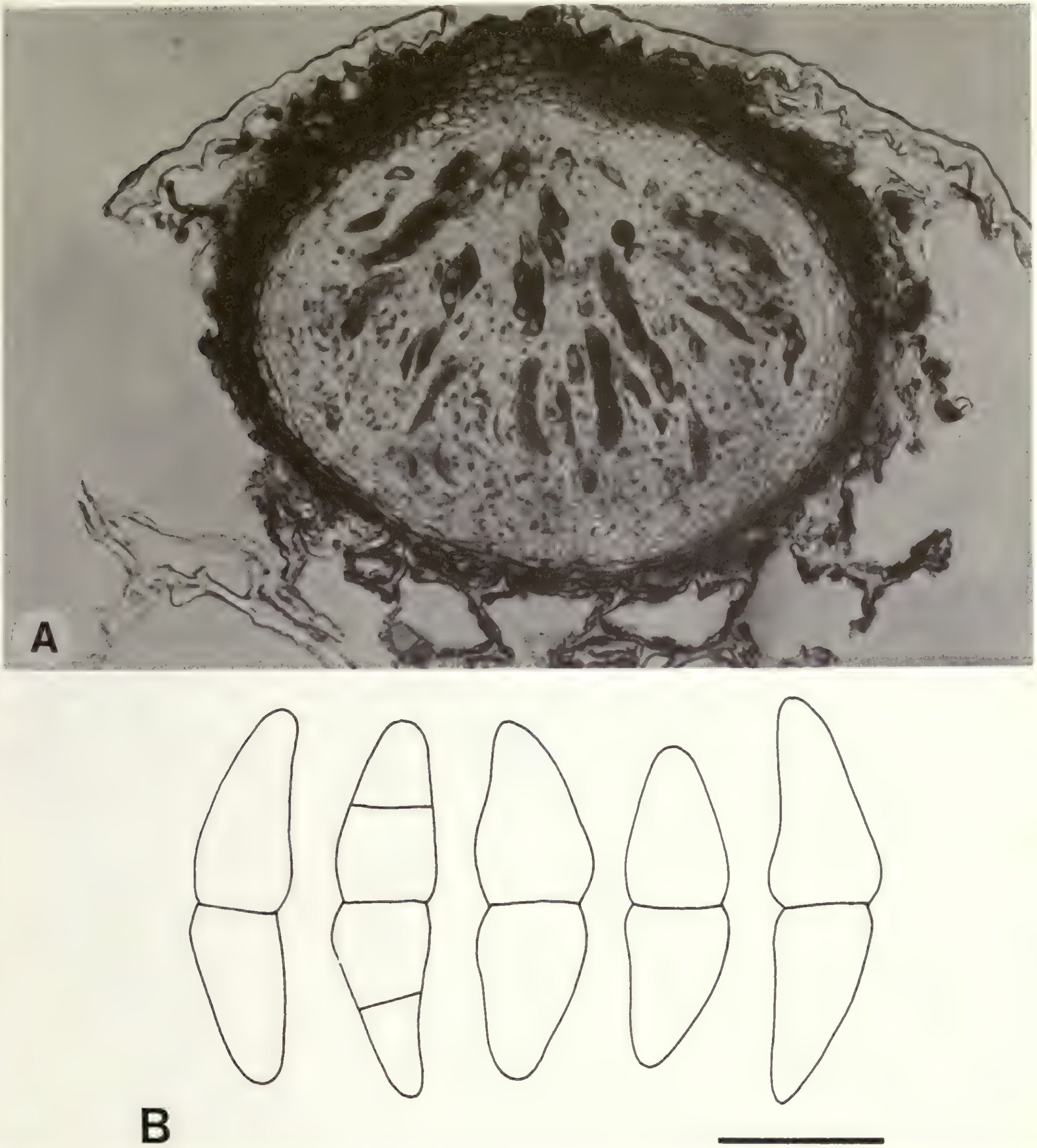


Fig. 68 *Verrucaria ribesiella* (Nurmes, H). **A**, Vertical section of ascoma, × 500. **B**, Ascospore outlines, scale = 10 μm.

brown, smooth-walled at maturity but sometimes appearing slightly verrucose within the asci, with a thin gelatinous sheath, (16–)19–22(–24) × (5–)6–7 μm.

Müller & von Arx (1962: 326) placed this taxon as a synonym of *Mycomicrothelia macularis* but it must be quite clear from the above short description that it has nothing to do with that species. The ascospore shape and septation recalls *Trematosphaeria pertusa* but the thinner walls, ascomatal shape, and especially the cellular paraphyses mean that it cannot be placed there. The ascospores lack the thick walls characteristic of *Massaria* de Not. and the fungus might most appropriately be interpreted as a brown-spored species of *Massarina* Sacc. None of the genera accepted in the main part of the present work appears suitable. In order to provide at least a temporary place for this interesting fungus I propose the new combination **Massarina ribesiella** (Nyl. ex Vainio) D. Hawksw., **comb. nov.** In my opinion *Massarina* is itself heterogeneous and in need of a thorough re-appraisal, at which time a more appropriate place for *M. ribesiella* can be expected to be found.

According to the original description, I suspect that *Massaria occulta* Rommell, which was described from *Ribes grossularia* in Sweden, may well be a later synonym of *Massarina ribesiella*, althought its ascospores were given as 20–28 × 8–9 μm.

Microthelia rimosicola Leighton ex Mudd, *Man. Br. Lich.*: 308 (1861).

Type: British Isles, Shropshire, 'Wrekin Hill', on *Rhizocarpon concentricum* (Davies) Beltr., *W. A. Leighton* [*Lich. Br. Exs.* 253] (BM—isotype).

Verrucaria rimosicola Leighton, *Lich. Br. Exs.* 253 (1856), nom. inval. (Art. 32.1).

For further obligate synonyms see Keissler (1930: 422).

This fungus produces black slightly erumpent ascomata 60–125 μm diam which are aparaphysate and produce ascospores which are 3-septate, markedly constricted at the septa, very pale brown when mature, with a gelatinous sheath, and measure 18–19 × 6·5–7 μm. Keissler (loc. cit.) placed this name as a synonym of *Phaeospora parasitica* (Lönnr.) Arnold and it certainly recalls that taxon as generally understood, but the spores are paler, somewhat larger and broader, more constricted, and have a well-developed gelatinous sheath. Leighton's collection is also conspecific with the monotype species of *Pyrenulella* Fink, *P. endococcoidea* (Nyl.) Fink (holotype studied), described from the same host. As *M. rimosicola* is the holotype species of *Phaeospora* Hepp (i.e. *P. rimosicola* (Leighton ex Mudd) Hepp), Fink's genus must be regarded as a synonym of *Phaeospora*. As an interim measure I propose that *P. parasitica* and *P. rimosicola* be retained as separate species; more detailed work is needed to establish whether they should be subsumed under the older epithet, i.e. *P. parasitica*.

Microthelia romeana Müll. Arg. in *Flora, Jena* **69**: 318 (1886).

This species was originally described from calcareous rocks in Switzerland and stated to have globose perithecia 100 μm wide, indistinct paraphyses, 50–60 spored asci, and 1-septate brown ascospores 6–8 × 2·5–3·5 μm. Keissler (1936: 55) examined the type material and considered it to be the species now known as *Muellerella pygmaea* (Körber) D. Hawksw., but the smaller perithecia and narrow spores, together with Müller's statement 'Apothecia minora et sporae graciliores quam in *[M.] pygmaeo*' leave little doubt that the species was the allied *M. lichenicola* (Sommerf. ex Fr.) D. Hawksw. (Hawksworth, 1979*a*: 289).

Didymosphaeria rubi Fuckel in *Jb. nassau. Ver. Naturk.* **23/24**: 141 (1870).

The combination '*Microthelia rubi* (Fuck.) Niessl' was mentioned by Scheinpflug (1958: 345) in a list of specimens examined but does not appear to have ever been validly published. Fuckel's taxon is now regarded as a synonym of *Didymosphaeria oblitescens* (Berk. & Broome) Fuckel (Scheinpflug, loc. cit.).

Microthelia rugulosaria Lindsay in *Trans. R. Soc. Edinb.* **25**: 540 (1869).

The holotype was studied by Hawksworth (*in* Pegler *et al.*, 1980: 513–515) who described and illustrated the species, gave an account of its synonymy, and made the combination *Polycoccum rugulosarium* (Lindsay) D. Hawksw.

Endococcus rugulosus Nyl. in *Mém. Soc. Imp. Sci. Nat. Cherbourg* **3**: 193 (1855), Art. 72 note 1.

Verrucaria rugulosa Borrer ex Leighton, *Br. Angioc. Lich.*: 47 (1851), nom. illegit. (Art. 64.1), non *V. rugulosa* Flörke in *Magazin Ges. naturf. Fr. Berl.* **2**: 306 (1808).
Microthelia rugulosa (Nyl.) Mudd, *Man. Br. Lich.*: 306 (1861).

This is the type species of *Endococcus* Nyl. The holotype specimen was examined by Hawksworth (1979*a*: 287) and the name taken up for the species previously known in recent years as *Tichothecium perpusillum* (Nyl.) Arnold. Obligate and taxonomic synonyms are compiled in Hawksworth (loc. cit.).

Microthelia scabrida Lahm *in* Körber, *Parerg. Lich.*: 399 (1865).

The holotype was studied by Hawksworth (1979*a*: 289) who found it to be a later synonym for *Endococcus stigma* (Körber) Stizenb.

Verrucaria scopularia Nyl. in *Notis. Sällsk. Fauna Fl. fenn. Förh.* **6**: 282 (1861).

Microthelia scopularia (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.* **2**: 105 (1880).

Examination of the holotype established that this was the earliest epithet for the species previously known as *M. aterrima* (Krempelh. ex Anzi) Zahlbr. It is now transferred to *Lichenothelia* as *L. scopularia* (Nyl.) D. Hawksw. (Hawksworth, 1981*b*: 147).

Microthelia sexlocularis Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **30** (3): 38 (1888).

Polythelis sexlocularis (Müll. Arg.) Clem., *Gen. Fungi*: 173 (1909).

The holotype of this name was described and illustrated by Hawksworth (1983*b*), who found that it represented a genus of Pyrenulaceae with both eu- and distoseptate ascospores. Clement (1909) introduced the generic name *Polythelis* Clem. for this fungus, but that name is pre-occupied by *Polythelis* J. C. Arthur introduced in 1906 for a genus of rusts. The new generic name **Polypyrenula** D. Hawksw., **nom. nov.** (replaced name: *Polythelis* Clem., *Gen. Fungi*: 173, 1909) and new combination **Polypyrenula sexlocularis** (Müll. Arg.) D. Hawksw., **comb. nov.**, are consequently introduced here for this fascinating species.

Microthelia shirleyana Müll. Arg. in *Rept Austral. Soc. Advmt Sci.* **6**: 455 (1895).

Type: Australia, Queensland, 1893, *J. F. Shirley* 1776 (G—lectotype).

Fig. 69A–C.

This taxon has very large ascomata to 450–700 μm diam, and to 500 μm tall in vertical section. A pronounced ostiolar canal extends from a subglobose locule with a thick pseudoparenchymatous red-brown wall through a well-developed involucrellum which involves host tissue. There are no algal cells evident. The locule is filled by a dense mass of filamentous, rarely branched, hyphae and apparently consists of paraphysoids 1–1·5 μm thick. The subcylindrical asci have ± uniseriate to almost distichously

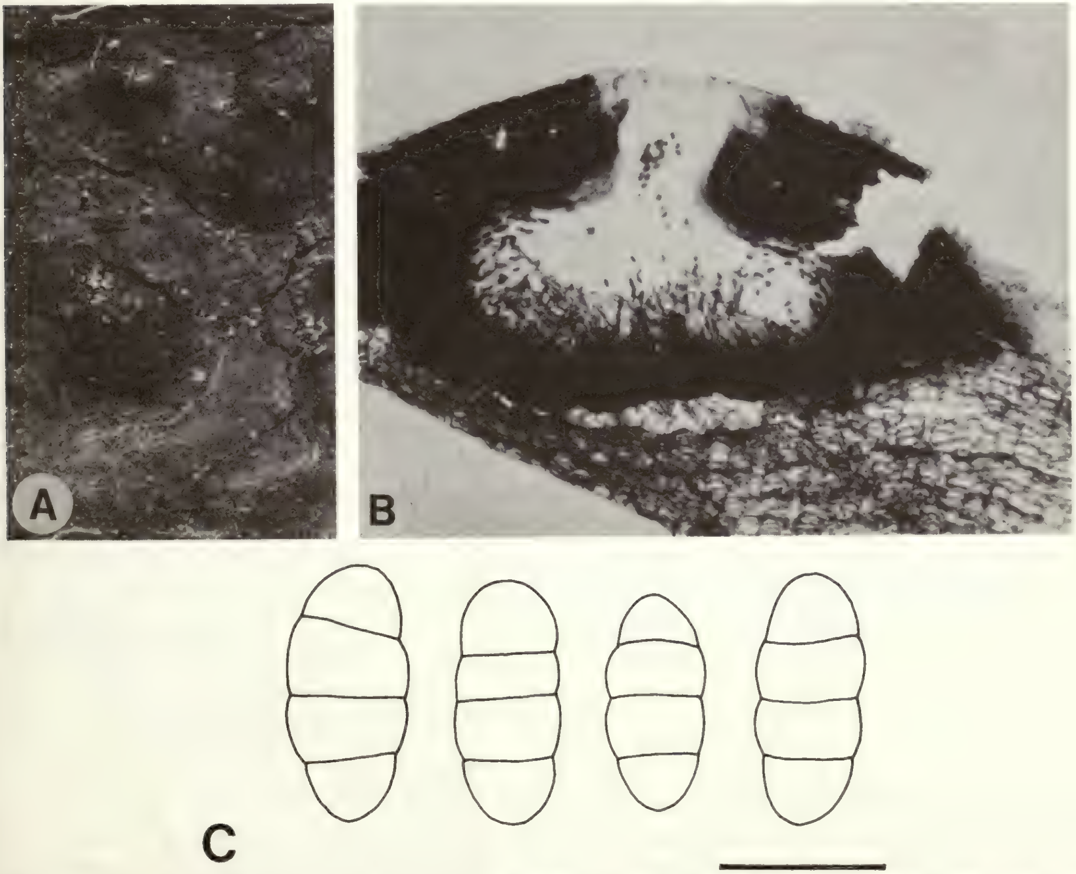


Fig. 69 *Microthelia shirleyana* (G—lectotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 100. **C**, Ascospore outlines, scale = 10 μm.

arranged ascospores and the ascospores themselves are red-brown, 3-septate, slightly constricted at the septa, with only a very slight gelatinous sheath, and measure 13–15 × 5·5–7 μm. Bitunicate discharge of the asci was not observed but at least the young asci have a thickened apex with an internal canal. Neither the asci nor the centrum turned blue in iodine. The fungus is evidently close to *Melanomma* but differs in the immersed ascomata which do not become erumpent. The taxon should be re-studied in the context of a monographic treatment of the tropical *Melanomma*-like fungi, and it would be premature to propose a new combination into that genus here.

Two collections were cited in the original account of this species. That made by Shirley is selected as lectotype here as this collection bears Müller's sketches and notes and provided the species epithet. The second collection (Australia: Queensland, *F. M. Bailey* 318, comm. C. Knight 1887, G) is conspecific with the lectotype.

Microthelia sierraleonensis Dodge in *Beih. Nova Hedwigia* **12**: 8 (1964).

This species was described from bark of *Funtumia africana* collected in Sierra Leone by F. C. Deighton but no material could be located in BM or K. *M. sierraleonensis* was described as lichenized with *Trentepohlia*, and stated to have perithecia 300 μm diam, slender dichotomously branched and evanescent 'paraphyses', evanescent asci 37 × 16 μm, and brown 1-septate ascospores 13–16 × 7–8 μm not constricted at the septum. The application of the name is currently uncertain, but the description of the asci and paraphyses indicate that the taxon probably does not belong to any of the genera accepted in the main part of this work.

Microthelia solorinaria Lindsay in *Q. Jl microsc. Sci.* II, **9**: 350 (1869).

The holotype material has recently been rediscovered and found to belong to *Rhagadostoma lichenicola* (de Not.) Keissler (see Hawksworth, 1981*c*: 78).

Microthelia stereocaulicola Lindsay in *Trans. R. Soc. Edinb.* **25**: 537 (1869).

The identity of this species was investigated by Hawksworth (1978*b*: 191–192) who found it to be a later synonym of *Polycoccum trypethelioides* (Th. Fr.) R. Sant.

Microthelia stictaria Lindsay in *Trans. R. Soc. Edinb.* **25**: 541 (1869).

Didymosphaeria stictaria (Lindsay) Sacc. & Trotter *in* Saccardo, *Syll. Fung.* **22**: 17 (1913).

This species was described as 'parasitic on thallus of *Sticta Freycinetii*, Del., Campbell's Island, Dr Hooker, Antarctic Expedition (sub-nom. *S. scrobiculata*)'. This material could not be located in E (B. J. Coppins, in litt.) or BM but could well have been filed under the host which was almost certainly a species of *Pseudocyphellaria* Vainio (other than *P. freycinetii* (Delise) Malme to judge from the locality). The ascospores were illustrated as ellipsoid, 1-septate, brown, and verruculose (Lindsay, loc. cit.: pl. 24 fig. 4a–b) so it is possible that he had a species of *Polycoccum*.

Microthelia stictaria Müll. Arg. in *Bull. Herb. Boissier* **3**: 326 (1895), nom. illegit. (Art. 64.1), non *M. stictaria* Lindsay in *Trans. R. Soc. Edinb.* **25**: 541 (1869).

Type: Australia, Victoria, Owens River, Snowy Creek, on *Pseudocyphellaria crocata* var. *esorediata* (Müll. Arg.) Vainio, 1894, *M. Cann* (G—holotype).

Examination of the holotype, filed under the host and not annotated as with this parasite in G, showed that it produced largely immersed aparaphysate ascomata and had ascospores which were hyaline at first but becoming pale brown when mature, smooth-walled, 1-septate, and 10·5–14 × 3·5–5 μm. The fungus is most appropriately regarded as a *Stigmidium* Trevisan species and, from the original description of *Pharcidia cupularis* Pat., might be identical to that species although its spores were said to remain hyaline. In view of the need for a thorough revision of *Stigmidium* no new name is proposed for Müller's fungus. It should be noted that *Microthelia stictaria* Lindsay (q.v.) had distinctly soleiform, verruculose, and reportedly smaller (8 × 3·5 μm) ascospores.

Microthelia striatispora Aebi, Harr & E. Müller in *Nova Hedwigia* **22**: 64 (1972).

The holotype of this fungus was studied by Hawksworth (1985*a*) who concluded that it was most appropriately referred to *Kirschsteiniothelia* as *K. striatispora* (Aebi, Harr & E. Müller) D. Hawksw.

Microthelia subfuscicola Lindsay in *Q. Jl microsc. Sci.* II, **11**: 39 (1871).

Type: British Isles, Scotland, S. Aberdeen, Braemar, Morrone [as 'Morchone'], on *Lecanora carpinea* (L.) Vainio, August 1856, *W. L. Lindsay* (E—holotype).

The above collection is almost certainly the holotype for this epithet as it is on the correct host (Lindsay's concept of '*L. subfusca* var. *albella*'), and bears the precise locality and collection details published by Lindsay. There is, however, no indication of the name *M. subfuscicola* on the specimen but scrutiny of it revealed that some fungi were present in apothecia and also that these had been cut for microscopic study in the past. It is clear that Lindsay not infrequently omitted to put his names on the specimens he based them on, perhaps often writing up data from his drawings and notes some years after the specimens were actually studied. Lindsay clearly intended to ascribe the epithet *subfuscicola* to a lichenicolous fungus rendering the host apothecia '. . . rough or verrucose, by the close aggregation of numerous conceptacles . . .' which included asci turning blue in iodine producing spores which were pale yellow, pyriform, and 1-septate. He also refers to a more deeply parasitic species blacking the apothecia but with the spores '. . . brown, 2-locular, and figure-8-shaped'.

The apothecia in the specimen prove to be infected by an *Arthonia* species, probably conspecific with *A. varians* (Davies) Nyl. (syn. *A. glaucomaria* (Nyl.) Nyl.), with 3-septate subhyaline ascospores 15–16·5 × 5–7 μm, together with the coelomycete *Lichenoconium lecanorae* (Jaap) D. Hawksw. (the pycnidia of which give the apotheca a verrucose appearance). As the diagnostic features of the taxon were primarily based on the former element, the name should be added to the synonymy of *A. varians* s. lat. Vouaux (1913: 217) and Keissler (1930: 73) placed Lindsay's name as a possible synonym of *A. clemens* (Tul.) Th. Fr., but in that species the ascospores are consistently 1-septate.

Microthelia subgregans Müll. Arg. in *Rept. Austral. Soc. Advmt Sci.* **6**: 455 (1895).

Type: Australia, Queensland, 1887, *C. Knight* 315 (G—holotype).

Fig. 70A–E.

This is a member of the *Arthopyrenia bifera*-group as understood by Harris (1975: 69–74). This does not belong to *Arthopyrenia* s. str. but appears, in my view, to be closer to the Trypetheliaceae as the hamathecium consists of paraphysoids. The asci are 2-spored in Knight's collection and the ascospores 43–49 × 17–18 μm; according to the original description the asci can also be 4-spored and the full spore range is 40–50 × 15–20 μm. The ascospores are at first 1-septate but later additional septa develop within the spore towards the apices and the wall is slightly verruculose. This species is very close to the tropical North American *A. bifera* Zahlbr., which also has a 2-spored asci and ascospores 37–48 × 15–16 μm, and may well provide an earlier epithet for it. However, I have not seen material of *A. bifera*, and the tendency of the ascomata in *M. subgregans* to be arranged in small groups might provide a specific criterion for their separation. These taxa may well require a new generic name, but in the interim it is appropriate to make the combination **Arthopyrenia subgregans** (Müll. Arg.) D. Hawksw., **comb. nov**.

Didymosphaeria thelenoides Vainio in *Ann. Acad. Sci. fenn.* A, **6** (7): 211 (1915).

Type: Dominican Republic, Dominica, 'ad corticem arboris in summo monte Conliabon', 3700 m, *W. R. Elliot* 1533 (not traced).

The original material on which the taxon was based could not be located in TUR (T. Lempiainen, in litt.), BM, or K. The ascospore dimensions (28–32 × 12 μm) suggest *Mycomicrothelia thelena*, but they were reported to become 3-septate. A further possibility could be *M. hemisphaerica*, but in that species the ascospores are narrower than reported for *D. thelenoides*. As no thallus was reported and the ascomata were said to be 0·5–1 mm wide, it seems unlikely that Vainio's name is an additional synonym of *M. thelena*. Until the type material is located his name must consequently be treated as of uncertain application.

Microthelia thelenula Nyl. ex Müll. Arg. in *Bot. Jb.* **6**: 416 (1885).

Type: Cuba, *C. Wright* [*Verr. Cub.* exs. 1] (G—holotype).

Verrucaria thelenula Nyl. in *Flora, Jena* **59**: 364 (1876), nom. inval. (Art. 32.1).
Kirschsteiniella ciferriana Petrak in *Annls mycol.* **30**: 191 (1932). Type: see p. 141.

Fig. 71A–F.

Wright's material from Cuba is probably conspecific with *Kirschsteiniella ciferriana* (p. 141), described from the Dominican Republic, and so provides an earlier name for it. The superficial ascomata are mainly 100–150 μm diam, the thallus is associated with algae but probably only fortuitously, and the ascospores

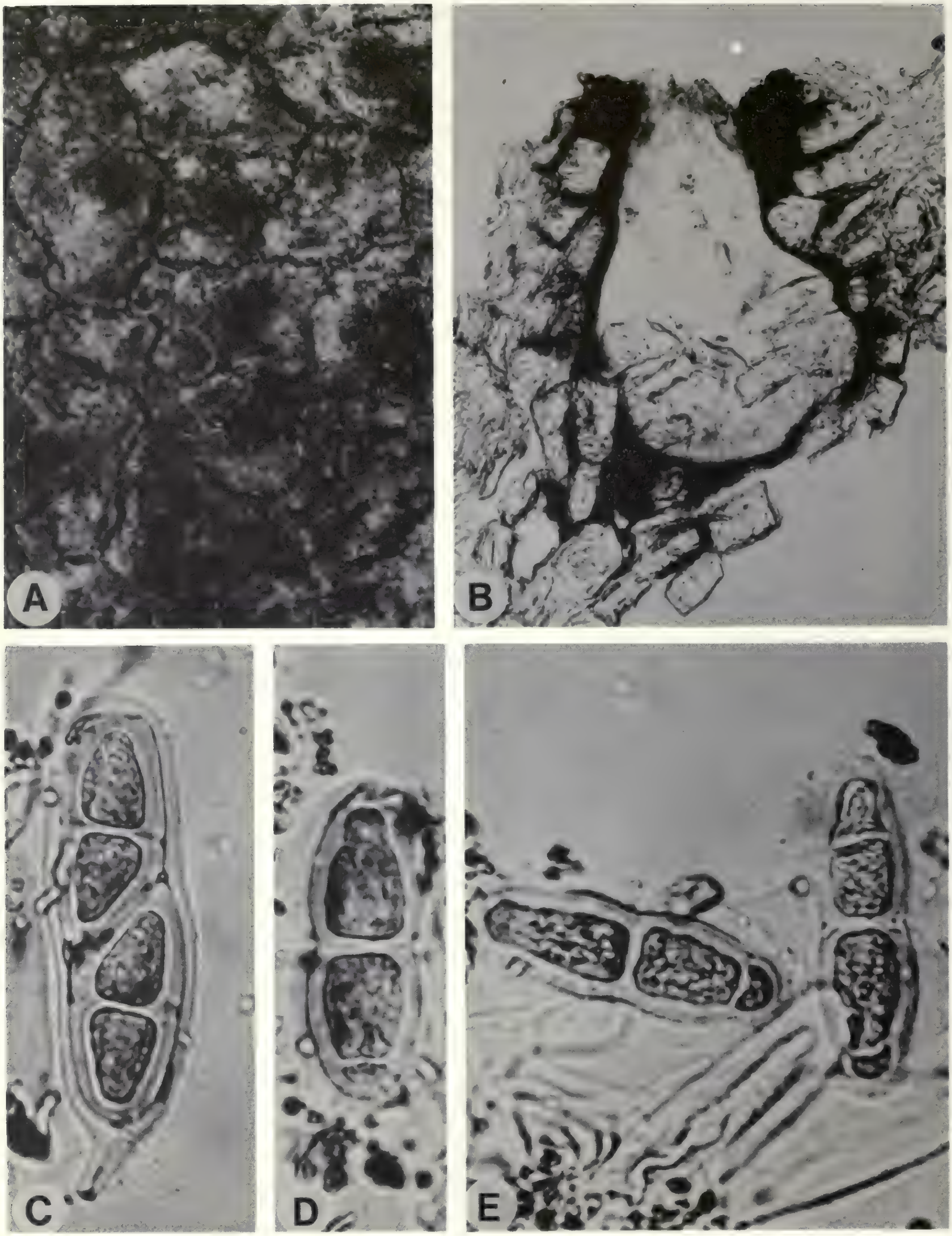
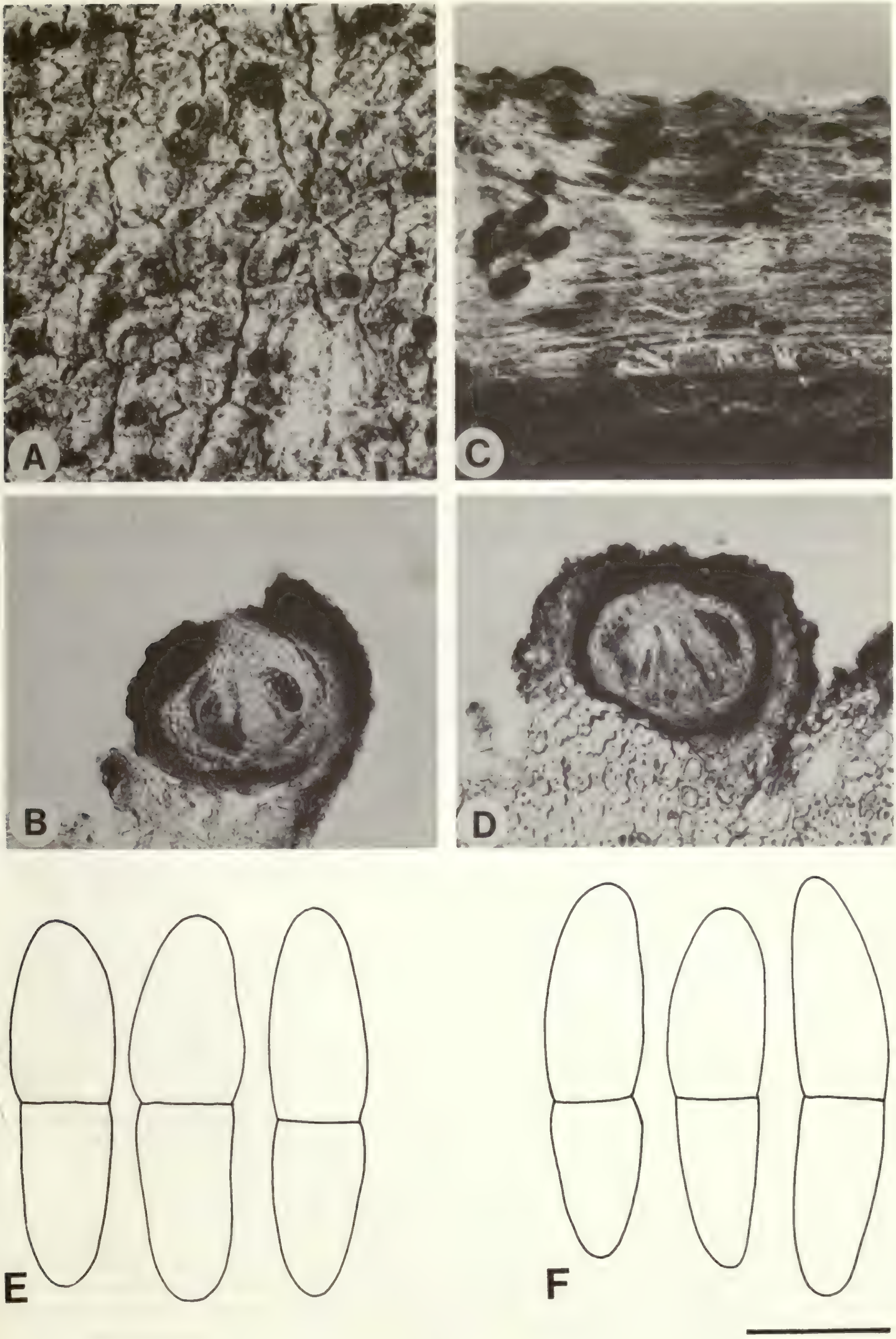


Fig. 70 *Arthopyrenia subgregans* (G—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250. **C**, Ascus containing two ascospores, × 1020. **D–E**, Ascospores, × 1020.

Fig. 71 (opposite) *Microthelia thelenula*. **A**, Surface view (G—holotype of *M. thelenula*), × 20. **B**, Vertical section of ascoma (material as **A**), × 250. **C**, Surface view (W-PETRAK 37104—holotype of *Kirschsteiniella cifferiana*), × 20. **D**, Vertical section of ascoma (material as **C**), × 250. **E**, Ascospore outlines (material as **A**). **F**, Ascospore outlines (material as **C**). Scale **E–F** = 10 μm.


A
B
C
D
E
F

are elongate-ellipsoid, verruculose, pale brown, 1-septate, sometimes guttulate and then appearing 3-septate, and (23–)25–28 × (5·5–)6·5–7(–8·5) μm, with a thin gelatinous sheath scarcely swelling in potassium hydroxide.

This is a very interesting fungus from the point of view of the structure of the ± superficial ascomata. These have an entire wall of dark brown radially compressed hyphal tissue, appearing almost pseudoparenchymatous in parts, surrounded by a subglobose to almost pyriform cavity (without a flattened base) but further, outside this wall, a massive clypeate structure comprising branching hyphae in a loose textura intricata; host cells are visible in the lower parts of the clypeus but difficult to see in the upper parts as they become occluded. The asci are unusual in that they have the lower part swollen and the upper extending into a long beak with a distinct channel in its lower spore-less parts; the asci are mainly 65–80 × 18–21 μm. The pseudoparaphyses are abundantly branched and anastomosed, cellular, persistent, and 2·5–3·5 μm wide.

It is possible that this fungus should be referred to *Mycomicrothelia* but I hesitate to place it there in view of the structure and globose shape of the mature ascomata and the possibility of similar taxa having already been described in *Didymosphaeria* s. lat.

Sphaeria thujina Peck in *Rep. Bot. N.Y. St. Mus.* **27**: 110 (1875 ['1873']).

Kirschsteiniella thujina (Peck) Pomerl. & Ether. in *Mycologia* **53**: 160 (1962 ['1961']).

The holotype of this fungus was studied by Hawksworth (1985*a*) who found that it was appropriately placed in *Kirschsteiniothelia* and combined it into that genus as *K. thujina* (Peck) D. Hawksw.

Microthelia triseptata Räsänen in *Arch. Soc. zool.-bot. fenn. Vanamo* **3**: 88 (1949).

Type: Philippine Islands, Samar, Catubig River, 'corticola', February/March 1916, *G. Edaño* 24931 (H—holotype).

Fig. 72.

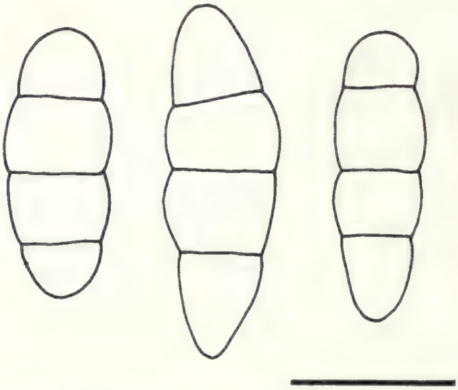


Fig. 72 *Microthelia triseptata* (H—holotype) ascospore outlines. Scale = 10 μm.

The type collection comprises conical ascomata mainly 700–900 μm diam, immersed only at the base, dimidiate, and containing cylindrical bitunicate asci which produce 3-septate reddish brown ascospores 14–21 × 5·5–7 μm; the ascospores are almost unseriate in the asci and the pseudoparaphyses scarcely branched and non-septate trabeculae. This fungus, which is definitely not lichenized, clearly belongs to *Melanomma* Nitschke ex Fuckel as interpreted by Samuels & Müller (1979). No new combination is made into that genus in view of the considerable number of taxa in it which require re-evaluation.

Microthelia marmorata var. **tubercularis** Norman in *Bot. Notiser* **1872**: 37 (1872).

As noted by Keissler (1936: 45), the original material on which this taxon was based ('in Alten Finmarkiæ inter Storvignæs & Öskarnæs ad rupes dolomiticas') is not present in O; it is also missing from TRH (S. Sivertsen, in litt.). The taxon seems to have lacked a distinct thallus but formed whitish-grey spots on the substrate, had branched and anastomosing paraphyses, 4–8 spored asci, and ascospores which were hyaline in the asci but 'elapsae demum fuscae'; no measurements of the spores were provided. It seems probable that Norman was dealing with a species of *Polycoccum*, but in the absence of the original material uncertainty must remain. Keissler (loc. cit.) mentions a specimen in O labelled by Norman as '*M. marmorata* sporis minoribus' which he tentatively referred to *M. minor* (see p. 158), but there is no evidence that that had anything to do with the epithet *tubercularis*.

Microtheliopsis uleana Müll. Arg. in *Flora, Jena* **73**: 195 (1890).

Microthelia uleana (Müll. Arg.) Schilling in *Hedwigia* **67**: 290 (1927).

The holotype in G and an isotype in UPS examined by Santesson (1952: 135) were not re-studied as from his account it is evident that *Microtheliopsis uleana* is quite unrelated to *Microthelia* and other taxa treated here (see p. 60 above).

Microthelia umbilicariae Lindsay in *Trans. R. Soc. Edinb.* **25**: 538 (1869).

Type: Norway, 'commercial pustulatous moss', on *Lasallia pustulata* (L.) Mérat (E—holotype).

Examination of the holotype showed that this fungus formed immersed perithecioid ascomata mainly 100–150 μm diam in gall-like swellings on the surface of the host thallus. Cellular pseudoparaphyses extending downwards from the upper part of the ascomatal cavity were clearly demonstrated in vertical section but difficult to discern in squash preparations. The ascospores are dark brown, ellipsoid, (0–)1-septate, not to only slightly constricted at the septum, rounded at the ends, smooth-walled, and 13·5–15 × (6–)6·5–7·5 μm. The peridium is composed of angular pseudoparenchymatous cells and the asci are 8-spored. The species is very close to *Polycoccum peltigerae* (Fuckel) Vězda (see Hawksworth, 1978*b*: 190), but differs in the broader, less or unconstricted ascospores which are also not attenuate apically. This is consequently best regarded as a further species of *Polycoccum* and the new combination **Polycoccum umbilicariae** (Lindsay) D. Hawksw., **comb. nov.**, is consequently made for it here.

Verrucaria umbonata Hepp *in* Zollinger, *Syst. Verz. ind. Archipel*: 9 (1854).

Type: Java, 'ad ramos dejectos', *H. Zollinger* 1549 (not traced).

This taxon is mentioned here as it was listed by Zahlbruckner (1921: 267) as a 'Species dubia' under *Microthelia*. The original description was very brief: 'th. membranaceus rufescens. Ap. hemisphaerica, mediocria; ost. umbonata. Spor. oblonga 2-loc. fusca, 18-4 mm'; a single ascospore was also illustrated (loc. cit., pl. I fig. 5(4)) which was almost black, 1-septate, and with the upper cell slightly larger. No material of this taxon could be located in BR (A. Bienfait, in litt.), G (O. Monthoux, in litt.), or L (A. K. Groenewegen, in litt.). In the absence of material the name must be treated as of uncertain application, but in view of its date the species epithet could well pre-date that of one of the species accepted in the present revision.

Microthelia uniserialis Zahlbr. in *Annls Cryptog. exot.* **5**: 199 (1932).

Type: South Africa, Knysna District, Hof van Eden, on smooth bark, *P. van de Byl* 869 (W 1934/328—holotype).

Fig. 73A–B.

This is a lichenized member of the Strigulaceae Fr. (sensu Harris, 1975) with a whitish crustose *Trentepohlia*-containing thallus, black erumpent *Arthopyrenia*-like ascomata with a clearly lateral ostiole, paraphysoids, and ascospores arranged strictly uniseriately in the asci. The ascospores remain hyaline for a considerable time but eventually become brownish, have a thin gelatinous sheath, verruculose walls, and measure 7–11 × 4–6·5 μm; an anamorph (? spermatial phase) is also present on the type specimen producing hyaline subcylindrical conidia mainly 2–3·5 × 1–1·5 μm. The genus *Pleurotrema* Müll. Arg. contains species with identical characters to *Microthelia uniserialis*, even having roughened ascospores, but the spores are normally hyaline in species of that genus. As I do not accept ascospore colour alone as a generic criterion (see p. 49), and as the ascospores of this species remain hyaline for some time, it should clearly be referred to *Pleurotrema*. As no member of that genus with such small and finally coloured ascospores has previously been recognized the new combination **Pleurotrema uniserialis** (Zahlbr.) D. Hawksw., **comb. nov.**, is made for this species here.

Microthelia ventosicola Mudd, *Man. Br. Lich.*: 307 (1861).

Type: British Isles, Yorkshire, Cleveland, Kildale Moor, on *Haematomma ventosum* (L.) Massal. thallus, *W. Mudd* [*Lich. Br. exs.* 300] (K—lectotype).

Verrucaria ventosicola (Mudd) Leighton, *Lich. Fl. Gr. Br.*: 463 (1871).

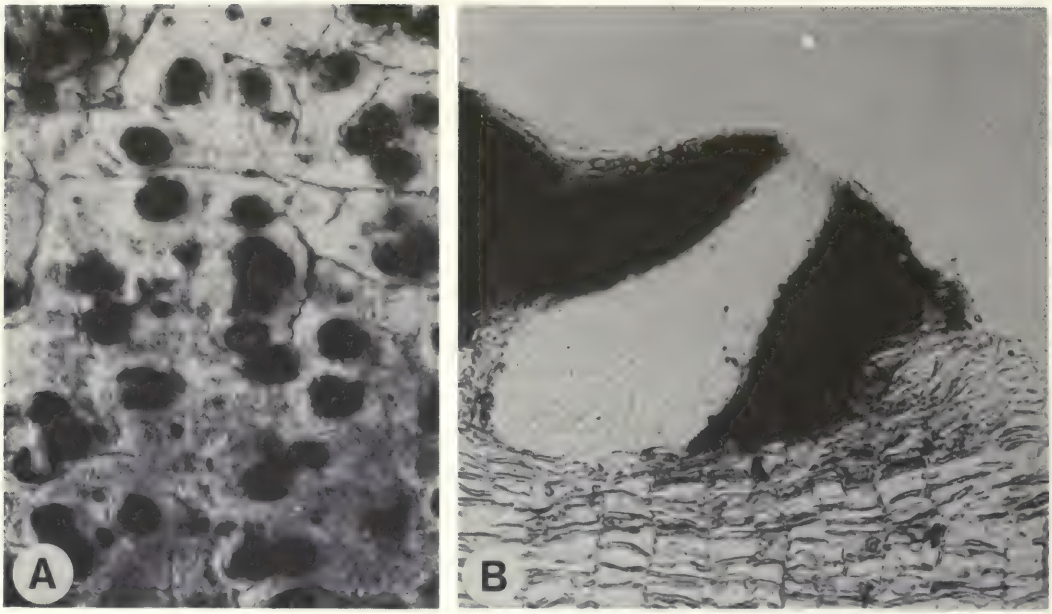


Fig. 73 *Microthelia uniserialis* (W 1934/328—holotype). **A**, Surface view, × 20. **B**, Vertical section of ascoma, × 250.

Tichothecium pygmaeum var. *ventosicola* (Mudd) Arnold in *Flora, Jena* **57**: 141 (1874).
Mycoporum pygmaeum var. *ventosicola* (Mudd) Jatta, *Syll. Lich. Ital.*: 495 (1900).

An examination of the lectotype showed that this species was a later synonym of *Muellerella pygmaea* (Körber) D. Hawksw. (see Hawksworth, 1979*a*: 289).

Lecidea vermicularia Lindsay in *Trans. R. Soc. Edinb.* **22**: 143 (1859).

Type: Falkland Isles, on *Thamnolia vermicularis*, 1842, *J. D. Hooker* (E—holotype).

Microthelia vermicularia (Lindsay) Lindsay in *Trans. Linn. Soc. Lond.* **27**: 319 (1869).
Tichothecium vermicularium (Lindsay) Arnold in *Flora, Jena* **57**: 142 (1874).
Karschia vermicularia (Lindsay) Rehm & Arnold in *Hedwigia* **42**: 174 (1903).
Discothecium vermicularium (Lindsay) Vouaux in *Bull. trimest. Soc. mycol. Fr.* **29**: 58 (1913).
Endococcus vermicularius (Lindsay) D. Hawksw. in *Bot. Notiser* **132**: 289 (1979).

When preparing my note on *Endococcus* Nyl. (Hawksworth, 1979*a*), the holotype of this epithet was not available for study. Subsequent examination of it showed previous descriptions to be misleading in several respects. The ascomatal cavity does have sparse knobby branched cellular pseudoparaphyses 1·5–2·5 μm thick, clearly seen in vertical sections (though not in squash preparations). Furthermore, the ascospores measure 14–18 × 7–9 μm, not 8–11 × 3–4 μm as stated in the literature, and have verruculose walls. It is therefore clear that this species is most appropriately placed in *Polycoccum*, and the new combination **Polycoccum vermicularium** (Lindsay) D. Hawksw., **comb. nov.**, is consequently made here. Whether the numerous ± equal-celled verruculose species currently referred to *Polycoccum* are really congeneric with the type species of the genus, *P. trypethelioides* (Th. Fr.) R. Sant., is a matter for future investigation. The latter species has very unequal-celled smooth ascospores (see Hawksworth, 1978*b*: 192 fig. 6D).

Microthelia verrucosaria Lindsay in *Q. Jl microsc. Sci.* II, **9**: 349 (1869).

For obligate synonyms see Keissler (1930: 455).

Lindsay (loc. cit.) based this name on the description of a fungus by Mudd (1861: 165) on a species referred to what is now known as *Pachysospora verrucosa* (Ach.) Massal. The material referred to by Mudd from Craig-na-Calliach and Ben Lawers could not be located in E (B. J. Coppins, in litt.) or BM. As the spores were described as 'ovate-oblong, or subclavate, bilocular, hyaline' and the paraphyses as 'capillary, distinct', it is unlikely to belong to any taxa accepted in the present revision.

Keissler (1930: 455) listed this name as a synonym of the fungus currently named as *Cercidiospora epipolytropa* (Mudd) Arnold, but this must be viewed as dubious. The application of Lindsay's name remains uncertain in the absence of the original material or re-discovery of a similar fungus on the same host.

Microthelia verruculosa Anastasiou in *Nova Hedwigia* **6**: 252 (1963).

Type: U.S.A., California, Salton Sea, on wood of *Tamarix aphylla* in salt marsh, 24 June 1961, *C. J. Anastasiou* RSA 23 (DAOM 109634—isotype).

The material in DAOM consists only of dried cultures and, while black bodies that could be young ascomata were present on a few of these, no mature ascomata were found. Also, the DAOM material was labelled as 'RSA 23 (TYPE)' on arrival, while 'RSA 26' was cited as the holotype; the latter was perhaps a 'lapsus'. According to Anastasiou (loc. cit.), a culture of this fungus was also sent to IMI for deposit but no record of it ever having been given an accession number could be found. The fungus was described as forming ascomata with a subglobose base and a much narrower elongated neck, 110–97 × 86–141 μm, asci which were bitunicate and 67·3–115·7 × 6·2–10·7 μm, and straw-coloured 1-septate ascospores 7·8–14·4 × 3·7–8·3 μm. It seems clear that this taxon does not belong to any of the genera accepted in the preceding parts of this revision, but its position must remain uncertain until further collections become available, enabling it to be critically examined.

Microthelia versispora Bagl. & Car. in *Atti Soc. Crittogam. Ital.* **2**: 337 (1881).

Type: Italy, 'ad saxa in monte Plaida supra Riva Vallisessiter', *F. Baglietto* (M—isotype).

Verrucaria versispora (Bagl. & Car.) Stizenb. in *Ber. tät. St. Gall. naturw. Ges.* **22**: 512 (1882).

Keissler (1936: 57) studied the holotype in MOD in which he found the spores to be only 1-septate and formed in 4–6 spored asci. The isotype I examined produced very dark brown coarsely ornamented 1-septate ascospores 28–32 × 11–12 μm, but I did not see any intact asci; a pencil drawing on the packet with this specimen, however, depicts 4-spored asci. Keissler referred this taxon to the species currently called *Polycoccum dzieduszyckii* (Boberski) D. Hawksw., but that species normally has only 2-spored asci (see p. 145). The centrum in the isotype does not turn blue in iodine indicating that this species does not belong to *P. marmoratum* (Krempelh.) D. Hawksw., which further has 8-spored asci, and also differs from *P. cartilaginosum* (see p. 141) in the number of spores in the asci. Baglietto's fungus consequently appears to represent a fourth species in the *P. marmoratum* group and the new combination **Polycoccum versisporum** (Bagl. & Car.) D. Hawksw., **comb. nov.**, is consequently proposed for it here. The ascomata are partially immersed in the whitish thallus of an indeterminate lichen. The number of spores in the ascus appears to be ± constant in each of the members of this group (i.e. 2 vs. 4(?–6) vs. 8) and, as variation in this character has not been found in one collection, this supports recognition at species rank.

Microthelia vesicularia Lindsay in *Trans. R. Soc. Edinb.* **25**: 543 (1869).

Type: Switzerland, on *Toninia caeruleonigricans* (Lightf.) Th. Fr., ex-hb. Hooker (BM—holotype).

Phaeospora vesicularia (Lindsay) Arnold in *Flora, Jena* **57**: 151 (1874).
Sphaeria vesicularia (Lindsay) H. Olivier in *Bull. internat. géogr. Bot.* **17**: 168 (1907).

Keissler (1930: 431) indicated that the type could not be found but it was located from the careful label transcription published by Lindsay (loc. cit.) amongst material filed under the host name now in BM. Superficial black carbonaceous perithecioid ascomata 100–200 μm arise almost superficially on the host thallus. These are aparaphysate and contain multi-spored asci forming 1–3-septate dark brown smooth-walled ellipsoid ascospores 12–15·5 × 5–7 μm. The ascus structure is typical of *Muellerella* Hepp ex Müll. Arg. and the species is therefore transferred to that genus as **Muellerella vesicularia** (Lindsay) D. Hawksw., **comb. nov.** This species forms a natural progression from the simple- and 1-septate spored species currently known in the genus, and its spores are consistently larger than those of the latter (see Hawksworth, 1979*a*: 286).

The species does not seem to be congeneric with the type species of *Phaeospora* (see p. 164) on the basis of ascus structure, early and deep pigmentation of the spores, and the absence of well-marked sheaths on the spores, in addition to the multi-spored asci.

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Dr P. B. Topham kindly carried out some statistical studies on the ascospores of selected species in an early phase of this work. We plan to extend this and present it as a joint contribution elsewhere.

Mrs C. Thatcher prepared the numerous microtome sections essential to work in this group; Mr D. Hobbs, Miss G. Godwin, and the late Mr D. Fry are thanked for help with the photographs; and Mrs P. Townson, Miss C. Martin, and Mrs M. Rainbow for clerical assistance.

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Index

This index includes all scientific names mentioned in the text, including those of photobionts and hosts. New taxa, and the page numbers of the principal references to accepted species, are printed in **bold**, accepted names in roman, and synonyms in *italic*. An asterisk (*) indicates pages on which there is a figure.

Abies 109
Acer saccharum 130
Acrocordia 59, 159
  gemmata 157, 159
Actinothecium 53
Adelococcus groedensis 124
Alnus incana 127
Amphisphaerella 150
  amphisphaerioides 150
  dispersella 149, 150
Amphisphaeria 45, 52, **53**, 133, 143
  alpina 133
  analeptoides 92
  betulina f. *pinicola* 133
  conica 143
  dothideaspora 82–84, 91
  emiliana 150
  inaequalis 83, 90–91
  incrustans 151
  lojkae 91
  maritima 153, 155
  melantera 156
  pachnea 108
  pinicola 133
  umbrina 143
Anastrophia rosei 141
Anisomeridium 45, 58, 132, 135, 138, 155
  biforme 44, 57, 138, 157
  magnosporum 155
Anzia 53, 57, 130
  aterrima 53
Araucaria angustifolia 134
Arnaudiella 53
  genistae 53
  ribis 92, 93*, 94*, 95
Arthonia 167
  arthonioides 147
  clemens 167
  glaucomaria 167
  varians 167
Arthopyrenia 49–50, 102, 133, 141–142, 167, 171
  ambulatrix 133
  apposita 68
  bifera 167
  calyciospora 139, 140
  cinerella 96
  clavaeformis 43, **142**
  conformis f. *rhypontoides* 161
  conspurcans 143
  furfuracea 147, 148*
  lapponina 120
  punctiformis 133
  rhyponta 134
  subgregans 43, **167**, 168*
Arthopyreniomyces 133
Aspicilia lacustris 150
Asterella 53
Asterotheca 53
Astrosphaeria 53
Astrosphaeriella 44, 46, 48, 49*, 51–52, **53**, 54*, 60, 130, 134–135, 147
  aosimensis 134, 146
  erumpens 146
  fuscomaculans 147
  fusispora 53, 54*, 147
  inaequalis 90
  pinicola 46, 133
  stellata 54*, 147
  trochus 54*
Astrotheca 53

Baeomyces rufus 133, 138
Betula 77, 79, 118, 132
  alba 118
Bignonia triphylla 150
Bonplandia trifoliata 115
Buellia anthracina 134
Buxus sempervirens 90

Canariopsis decumanii 138
Catillaria arthonioides 147
Cercidiospora epipolytropa 173
Cinchona 115
Clypeococcum 52, 53, 152
  cladonema 53, 55*
Cocos nucifera 145, 159
Collema muscicolum 142
Corylus 72, 79, 80
  avellana 70, 72, 77
Crataegus 96, 99
  germanica 96
Crotonis cascarillae 144
Cryptodidymosphaeria 53
  conoidea 54
Cyclothyrium 57, 134
Cytisus 156
  laburnum 156

Daphne 66, 95
  mezereum 95
Dendryphiopsis 125
  atra 47
Didymascina 53
  futilis 54
  salicicola 54
Didymella 141
Didymosphaerella 54
  filicina 54
Didymosphaeria 44–47, 52, **54**, 56–57, 59, 62, 65, 144–145, 157, 170
  alpina 133
  analeptoides 46, 92
  araucana 134
  atomaria 135
  calyciospora 43, **141**
  crastophila 144
  dannenbergii 121
  detincta 99
  donacina 144
  epidermidis 54–56
    f. *crataegi* 96
    f. *mespili* 96
  fuliguncta 121
  futilis 55*, 56, 134, 144, 153, 157, 159

Didymosphaeria – *cont.*
  galiorum 55
  genistae 55
  haplospora 149
  grandiuscula 124
  melanospora 95
  micula 46, 157
  oblitescens 57, 144, 164
  parietinaria 159
  peltigerae 55
  perrugosaria 159
  pteridina 54
  puyae 160
  ribesiella 46, 161
  rubi 164
  rubicola 134, 141, 150
  rubri 55
  stictaria 166
  thelenoides 167
  verrucariaeformis 96
  wallrothii 46, 115
  xylostei 55
Dipyrenis 56
  brachysperma 56
Discothecium calcaricola 139
  gemmiferum 160
    var. *calcaricola* 139
  vermicularium 172
Dothivalsaria 52, 56
  megalospora 56

Endococcus 45, 52, **56**, 146, 153, 164, 172
  atricola 138
  calcareus 139
  calcaricola 139
  exerrans 146
  gemmiferum 147
  parietinarius 159
  parietinus 159
  propinquus 45, 147, 160
  ramalinarius 161
  rugulosus 56, 139, 153, 164
  stigma 164
  vermicularius 172
Eopyrenula leucoplaca 118, 147
Ephedra major 153
Epicymatica verrucariaeformis, 96, 99
Eucalyptus pauciflora 146
Evernia prunastri 160

Ficus carica 129
Fraxinus 79, 120
  excelsior 77
Funtumia africana 166

Graphis scripta 153
Guayacia officinalis 148

Haematomma ventosum 171
Haplovalsaria 56
  simplex 56
Hymenelia lacustris 150

Ilex 79
  aquifolium 77

Jahnula 46, 49*, 51–52, **56**
  aquatica 56

Karschia 47
  vermicularia 172
Kirschsteiniella 46, **57**, 130, 153
  applanata 134
  californica 90–91, 92*
  canariensis 140*, 141
  ciferriana 141, 167, 169*
  conica 143
  inaequalis 90
  macedonica 153
  thujina 170
Kirschsteiniothelia 44, 47, 49*, 50, 51–52, **57**, 121, 153, 170
  aethiops 46, 57, 58*, 62, 78, 125, 133–134, 151, 153, 156
  maritima 155
  striatispora 166

Lasallia pustulata 171
Lecanora atra 137
  carpinea 167
  populicola 159
  subfusca var. albella 167
Lecidea 147
  alectoriae 158
  arthonioides 147
  petraea 160
  vermicularia 172
Leiophloea 133
  lyellii 153
Leptogium teretiusculum 142
Leptorhaphis 59–60, 64, 137
  atomaria 44, 130, **135**
  epidermidis 132
  tremulae 137
    var. *lucida* 130
Leptosphaeria 44
Leucocarpia 138
Lichen analeptus 133
  atomarius 135, 137
  cinereo-fuscus 133
  olivaceus 133
Lichenoconium cargillianum 141
  erodens 160
  lecanorae 167
Lichenosticta alcicornaria 132
  podetiicola 132
Lichenothelia 44, 48, 49*, 51–53, **57**, 58*, 59, 121, 156, 165
  metzleri 58*, **156**
  scopularia 57, 134–135, 137, 144, **165**

Massaria 163
  occulta 164
Massariella oleae 130
Massariellopsis 57
  aprutina 57
Massarina 125, 163
  ribesiella 43, **163***, 164
Massariopsis 45, 57
  crastophila 144
  wallrothii 115

Maximiliana regia 60
Melanomma 159, 166, 170
  oxysporum 43, **159**
  pulvis-pyrius 153
Melanospora macularis 92
Melanotheca macularis 92
Melaspilea 147
  arthonioides 146
  proximella 147
Mespilus germanicus 96, 98–99
Micarea 47
Microglaena 138
  biatorella 138
Micropeltis erumpens 146
Microthelia 43–48, 49*, 50, 52–53, 56, **57**, 58–60, 62, 121, 130, 133, 137–138, 142, 150, 153, 171
    sect. *Atomariae* 59
    sect. *Ecatanosporae* 59
    sect. *Holothelia* 46, 59
    sect. *Membranaceae* 59
    sect. *Hemithelia* 46, 57, 59
    sect. *Miculae* 57, 59
  adspersa 130
  alba 106, 107*, 108*
  albidella 112, 113*, 114*, 115
  alcicornaria 132
  ambigua 133
  ambulatrix 133
  analeptoides 92, 95
  analtiza 134
  anonacea 67
  anthracina 134
    f. *pallidior* 159
  aosimensis 134
  applanata 134
  apposita 68, 70
  araucana 134
  araucariae 134–135
  arctata 135
  asiatica 135, 137*
  aterrima 46, 135, 159, 165
    f. *atramentea* 46
    f. *pallidior* 159
    var. *dermatinoides* 46, 144
  atomaria 44–46, 56, 59–60, 96, 98–99, 135
    f. *calyciospora* 46, 139
  atramentea 137
  atricola 137
  aurora 138, 139*, 150, 155
  baeomycearia 138
  betulina 46, 115, 116*, 117*, 118
    f. *populicola* 115, 117*, 118
  biatorella 138
  biformis 45, 138, 143
  binucleolata 138
  brisbanensis 106, 107*, 108*
  calcaricola 139
  calyciospora 139, 140*, 148*
  captiosa 73
  cargilliana 141
  cartilaginosa 141
  cinerella 96, 115, 142
    f. *megaspora* 124, 125
  clavaeformis 142

collemaria 142
confluens 75
conothelena 81
  var. *errans* 81
conspurcans 143
cookei 143
crastophila 144
delitschia 144
diplospora 144
dispora 144
  f. *octospora* 158
dissepta 144
dominans 144, 145*
donacina 144
dotyi 145
dzieduszyckii 145
ecatonspora 59, 146
  var. *athallina* 135
elata 146
erumpens 146
exerrans 146
exigua 84–86
farrea 146
flavicans 73*, 74*, 75
fuliguncta 121, 123*, 124, 161
fumosula 86
furfuracea 147
fuscomaculans 147
fusispora 147
gemmifera 147
glabrata 147
  var. *coryli* 143
grandiuscula 124–125, 127, 128*
guayaci 149
haplospora 149, 150
hemisphaerica 86, 89–90
heterospora 150
hymenothora 138, 150
inaequalis 90
incrustans 151
innata 151, 152*
inops 153
intercedens 74–75, 86, 89*, 90
intermedia 84*, 85*, 86
knightiana 101–102
koerberi 95, 99
leightonii 153
leucothallina 112, 113*, 114*, 115
linderi 153
macquariensis 153
macrocarpoides 138, 150, 153, 154*
macularis 45–46, 92, 93*, 94*, 95
  f. *ribesiella* 46, 161
maculiformis 95
magnifica 155
maritima 153, 155
marmorata 46, 155, 171
  f. *cartilaginosa* 46, 141
  f. *minor* 46, 158
  var. *tubercularis* 170
melanospora 96
melanostigma 156
melasperma 156
membranacea 59, 127, 156
metzleri 46, 156
  f. *anthracina* 134
  var. *pallidior* 159
microsperma 156, 157*
micula 44–46, 56, 57, 59, 78, 124, 133, 143, 153, **157**
  f. *furfuracea* 147
  f. *grandiuscula* 46, 124
  f. *macrospora* 125
  var. *megaspora* 124
  var. *quadriloculata* 161
miculiformis 99, 100*, 101
  var. *detincta* 99, 100*, 101
minor 158, 171
minutula 102
minutissima 101
nephromaria 158
nonensis 105
oblongata 115, 116*, 117*, 118
obovata 106
oleae 127, 130
oxyspora 158*
pachnea 46, 108, 110
palavana 59, 159
parietinaria 159
perrugosaria 159
peripherica 159
petraeicola 160
pharaonis 160
ploseliana 160
propinqua 44–45, 160
prunastraria 160
prunastria 160
puyae 160
pygmaea 44–45, 58, **160**
queenslandica 107, 161, 162*
ramalinaria 161
rhypontoides 124, 161
ribesiella 95, 161
rimosicola 164
romeana 164
rubi 164
rugulosa 164
rugulosaria 164
scabrida 164
scopularia 46, 59, 164
sexlocularis 46, 132, 165
shirleyana 165*
sierraleonensis 166
socialis 110
solorinaria 166
stereocaulicola 166
stictaria 166
striatispora 166
subfallens 111
subfuscicola 167
subgregans 167
thelena 112
  var. *albicans* 130, 131*, 144
  var. *albidior* 130
  var. *subtriseptata* 112, 114*, 115
thelenula 141, 167, 169*
triseptata 170*
tubercularis 171
uleana 171
umbilicariae 171
uniserialis 171, 172*
vermicularia 172
verrucosaria 172
verruculosa 173
vesicularia 173
versispora 59, 173
wallrothii 115, 118
willeyana 119
Microtheliomyces 60
  atomariae 136
Microtheliopsis 60
  uleana 60, 171
Microtheliopsidomyces 60
Mimulus glutinosus 83–84
Montagnula 159
Muellerella 45, 52, 59–60, 130, 135, 138, 156, 161, 173
  atricola 138
  lichenicola 130, 135, 138, 142, 143, 146, 164
  polyspora 60
  pygmaea 45, 161, 164, 172
  vesicularia 43, **173**
Mycomicrothelia 43–44, 46, 48, 49*, 50–52, 60–63, **64**, 65, 78, 82, 83, 98, 102, 118, 121, 130–131, 137, 146, 170
  anonacea 43, 66, **67***
  apposita 43, 65, **68**, 69*
  atlantica 43, 63, 66, **70**, 71*, 72*, 78
  atomaria 46, 64, **135**, 137
    f. *calyciospora* 139
  captiosa 43, 66, **73***, 74*, 90, 101–102, 105, 120
  confluens 43, 65, **75**, 76*, 77*, 105
  confusa 43, 48, 63, 66, 70, 72, **76**, 78*, 79*, 80*, 98–99, 109, 120
  conothelena 43, 65, **81***, 115
  dothideaspora 43, 65, **82**, 83*
  eucalyptinum 146
  exigua 66, **84***, 85*, 101
  fumulosa 43, 66, 85, **86**, 87*, 101
  hemisphaerica 65, **86**, 88*, 89*, 90, 107, 167
  inaequalis 65, 83, **90**, 91*, 92*, 129
  macularis 45–46, 49*, 53, 63–64, 66, 70, 85–86, **92**, 93*, 94*, 95, 99, 163
    f. *ribesiella* 161
  melanospora 45, 48, 63, 66, **95**, 97*, 98*, 99, 137, 142
  micula 157
  miculiformis 43, 66, **99**, 100*
  minutissima 65–66, 101, 102*
  minutula 43, 66, 85, 86, **102**, 103*, 111
  modesta 43, 63, 65, 104*, **105**
  nonensis 43, 66, **105***, 142
  obovata 43, 65, **106**, 107*, 108*, 115, 161
  pachnea 43, 66, **108**, 109*, 146
  palmarum 159
  socialis 43, 49, 65, 75, **110***, 111
  subfallens 43, 66, 85, 101, 103, **111**, 112*

Mycomicrothelia – *cont.*
  thelena 43, 48, 49*, 63, 65, 70, 76, 90, 105, 106, **112**, 113*, 114*, 142, 167
  wallrothii 48, 57, 63, 68, 83, 95, 99, 111, **115**, 116*, 117*
  willeyana 43, 63, 66, 102, **119***
Mycoporum marmoratum 155
  pygmaeum var. *ventosicola* 172
Mycopyrenula 144
  coryli 143

Neuropogon 158

Olea 153
  europaea 90–91, 129–130

Pachysospora verrucosa 172
Parmelia olivacea 133
  pulla 55*
Peltigera rufescens 61
Pemphidium 60
  erumpens 146
  nitidum 60
Peridiothelia 43–44, 46, 49*, 50–52, 60, 62–63, **120**, 121, 124
  fuliguncta 43, 45, 60, 78, **121**, 122*, 123*, 125, 142, 157
  grandiuscula 43, 121, **124**, 125, 126*, 127*, 128*, 142, 156
  oleae 43, 121, **127**, 129*, 130
Pertusaria 124
  flavida 124
Phaeospora 173
  parasitica 133, 159, 160, 164
    f. *dzieduszyckii* 145
  rimosicola 164
  vesicularia 173
Phaeosporis 156
  melasperma 156
Phaeothyriolum 61
  eucalyptinum 61, 146
Pharcidia cupularis 166
  lacustris 150
Pittosporum floribundum 86
  glabratum 86
Placopsis 160
  gelida 160
  perrugosaria 159
Plagiocarpa 139, 150
  macrocarpoides 150
Pleospora 44–45, 159
  peripherica 144, 159
Pleurotrema 171
  uniserialis 43, **171**
Polyblastiopsis falliciosa 161
Polycoccum 52–53, 59, 61, **62**, 141, 145, 150, 152, 155, 158, 160, 166, 170–172
  cartilaginosum 43, **141**, 173
  dannenbergii 121
  dzieduszyckii 144–145, 173
  innatum 43, 151, **152**
  marmoratum 141, 155, 158, 173
  microstictum 158
  peltigerae 61*, 171
  rugulosarium 164
  sauteri 62
  squamarioides 160
  trypethelioides 166, 172
  umbilicariae 43, **171**
  vermicularium 43, **172**
  versisporum 43, **173**
Polypyrenula 43, **165**
  sexlocularis 43, **165**
Polythelis 46, 62, 165
  sexlocularis 62, 165
Populus 109, 118, 150
  tremula 130
Protoblastenia 135
  incrustans 135
Pseudocyphellaria 166
  crocata var. esorediata 166
  freycinetii 166
Puya chilensis 160
Pyrenidium actinellum 138
Pyrenillium 133
Pyrenula 52, 56–57, **62**, 130, 149
    sect. Pseudacrocordia 56
  biformis 124, 138
  chlorospila 61*
  cinerella 96
    subsp. *quadriloculata* 161
    var. *quadriloculata* 161
  coryli 143
  guayaci 149
  laevigata 148
  melanospora 95, 96, 97*, 98*, 99
  nitida 62
  oblongata 115
  obovata 106
  wallrothii 115, 117*, 118
  willeyana 119
Pyrenulella 164
  endococcoidea 164

Quercus 77, 79, 158
  ilex 129
  undulata 156

Rhagadostoma lichenicola 166
Rhizocarpon 159
  concentricum 144, 164
  obscuratum 160
  petraeum 144
Rhynchostomopsis 62
  brasiliensis 62
Ribes grossularia 162, 164
Rinodina aterrima 134–135
  bischoffi 153
Ribes 66, 95
  alpinum 95
  petraeum 95
Rubus sanctus 134

Schizophragma integrifolium 103
Schoepfia jasminodora 103–104
Sesleria caerulea 144
Seynesia 146
  erumpens 146
  Sorbus 79–80
  aucuparia 77
Sphaeria diplospora 144
Sphaeria applanata 57, 134
  leveillei 143
  thujina 170
  vesicularia 173
Sphaeropsis 143
  conica 143
Sphaerulina nephromaria 158
Splanchnonema 52, 62, 135, 156
  melanterum 62, 156
  pustulatum 62
Sporoschizon 133
Sticta freycinetii 166
  scrobiculata 166
Stigmidium 166
  dispersum 143

Tamarix aphylla 173
Tichothecium 45, 53, 58–59, **62**
  calcaricola 139
  collemarium 142
  dannenbergii 121, 123*, 124
  gemmiferum 160
  lichenicola 143
  marmoratum 155
  nigrescens 45
  perpusillum 164
  pygmaeum 160
    var. *ventosicola* 172
  vermicularium 172
Tilia 124, 143, 157
  platyphyllos 124
Tomasellia macularis 92
Trachylia 147
Trematosphaeria 143
  confusa 143
  pertusa 143, 163
Trentepohlia 52, 64, 70, 75, 77, 82, 89, 101–102, 106, 109, 115, 120, 155, 166, 171
Trichothecium 45, 59

Valsaria bignoniae 150
Venturia 160
Verrucaria 45, 53, 57, 59, 62, 141
  ambulatrix 133
  analeptoides 92
  analtiza 134
  apposita 68
  arctata 135, 136*
  atomaria 99, 135
  baldensis 144
  biformis 124, 138, 157
  binucleolata 138
  captiosa 73*, 74*, 75
  cinerea 99
  cinerella 45, 96, 97*, 142
    f. *micula* 157
    var. *megaspora* 124, 127, 128*
  clavaeformis 106, 140*, 142, 148*
  confluens 75
  conformis f. *rhypontoides* 161
  confusa 143, 148*
  conothelena 81–82
    var. *errans* 81–82
  conspurcans 143

dissepta 144
epidermidis var. *albissima* 132
farrea 146
fuscoatra 45, 59
gemmifera 147
glabrata 147
guayci 148, 149*
holopolia 150
hymenothora 150, 151*, 155
laevigata 148
leightonii 153
lyellii 153
magnifica 155
magnospora 155
melasperma 156
microthelena 84, 86
micula 157
  var. *cinereolutescens* 95, 99
  var. *megaspora* 124
  var. *furfuracea* 147
miculiformis 99
  var. *detincta* 99
  var. *distincta* 99
minutissima 101–102
muralis 143
nigrescens 45, 59, 62, 143
nonensis 105–106
obovata 106, 107*, 108*
olivacea 133
peripherica 159
pharaonis 160
populicola 137
punctata 99
punctiformis 99
ribesiella 161, 163*
rimosicola 164
rugulosa 164
scopularia 164
stigmatella 99
thelena 112, 114*, 115
  var. *albidior* 130, 132*
thelenula 167
umbonata 171
ventosicola 171
versispora 173
wallrothii 115

Xanthoria parietina 159

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Christopher R. Fraser-Jenkins

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A classification of the genus *Dryopteris* (Pteridophyta: Dryopteridaceae)

Christopher R. Fraser-Jenkins

c/o Department of Botany, British Museum (Natural History), Cromwell Road, London
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Contents

- Synopsis 183
- Higher classification and relationships of *Dryopteris* 184
- Classification within *Dryopteris* 186
- Taxonomy 187
  - *Dryopteris* Adans. 187
    - Subgenus 1. *Pycnopteris* (T. Moore) Ching 189
    - Subgenus 2. *Dryopteris* 189
      - Section 1. *Hirtipedes* Fraser-Jenkins 190
      - Section 2. *Fibrillosae* Ching 190
      - Section 3. *Pandae* Fraser-Jenkins 191
      - Section 4. *Dryopteris* 191
      - Section 5. *Remotae* Fraser-Jenkins 192
      - Section 6. *Pallidae* Fraser-Jenkins 192
      - Section 7. *Splendentes* Fraser-Jenkins 193
      - Section 8. *Cinnamomeae* Fraser-Jenkins 193
      - Section 9. *Marginatae* Fraser-Jenkins 194
      - Section 10. *Aemulae* Fraser-Jenkins 194
      - Section 11. *Lophodium* (Newman) C. Chr. ex H. Itô 195
    - Subgenus 3. *Erythrovariae* (H. Itô) Fraser-Jenkins 195
      - Section 1. *Erythrovariae* 196
      - Section 2. *Politae* Fraser-Jenkins 196
      - Section 3. *Variae* Fraser-Jenkins 196
    - Subgenus 4. *Nephrocystis* (H. Itô) Fraser-Jenkins 197
      - Section 1. *Purpurascentes* Fraser-Jenkins 197
      - Section 2. *Nephrocystis* 198
- Species not placed in the classification 198
- New species 199
- Hybrids 206
- List of synonyms 207
- Acknowledgements 213
- References 213
- Taxonomic index 216

Synopsis

The history of the higher and infrageneric classification of *Dryopteris* is briefly discussed and followed by a new classification of the genus into four subgenera, two of which involve new states: *Erythrovariae* (H. Itô) Fraser-Jenkins and *Nephrocystis* (H. Itô) Fraser-Jenkins. Within the subgenera 16 sections are recognised, the following 11 being new: *Hirtipedes* Fraser-Jenkins, *Pandae* Fraser-Jenkins, *Remotae* Fraser-Jenkins, *Pallidae* Fraser-Jenkins, *Splendentes* Fraser-Jenkins, *Cinnamomeae* Fraser-Jenkins, *Marginatae* Fraser-Jenkins, *Aemulae* Fraser-Jenkins, *Politae* Fraser-Jenkins, *Variae* Fraser-Jenkins, and *Purpurascentes* Fraser-Jenkins. The world's species of *Dryopteris* (*c.* 225) are placed in the various sections and in connection with these a full list of synonyms is included. A list of 89 hybrids is also given. Two new combinations, *D. crassirhizoma* Nakai subsp. *whangshangensis* (Ching) Fraser-Jenkins and *D. goldiana*

Bull. Br. Mus. nat. Hist. (Bot.) **14** (3): 183–218 Issued 30 January 1986

(Hook.) A. Gray subsp. *monticola* (Makino) Fraser-Jenkins, are made and *D. reichsteinii* Fraser-Jenkins is a new name for *D. paleacea* var. *madagascariensis* C. Chr. The species *D. parrisiae* Fraser-Jenkins, *D. ruwenzoriensis* C. Chr., *D. subpycnopteroides* Ching ex Fraser-Jenkins, and *D. tingiensis* Ching & S. K. Wu ex Fraser-Jenkins are described.

Higher classification and relationships of *Dryopteris*

Phyletic and cytogenetic details of *Dryopteris* and its relatives have been discussed in detail by Lovis (1977), who concludes that the genus is probably of dennstaedtioid origin, though the cytological evidence from the base number of 41 is not sufficient to resolve this question. Little fossil evidence for the origin of the dryopteroid ferns exists except for a tertiary fossil, *D. meeteetseana* R. W. Brown (see Lovis, 1977: 251). *Dryopteris* itself may well be of tertiary origin and appears to be relatively ancient, as may be deduced from the existence of a number of widely distinct subgenera within it.

The higher classification of the groups containing *Dryopteris* was set out by Pichi Sermolli (1973, 1977), and a brief survey is included here. In common with a great many other genera, members of the modern genus *Dryopteris* were at one time placed in the family Polypodiaceae which was a vast compendium of many different groups. By the beginning of the present century, the family group had been narrowed down to the Aspidiaceae Mett. ex Frank in the wide sense, which contained both the thelypteroid and aspidioid ferns, many of these being lumped together with *Dryopteris* species into the genera *Nephrodium* or *Lastrea*, or into *Dryopteris* itself. Christensen (1913*a*, 1920), in his monograph of tropical American *Dryopteris* (see also Christensen, 1938), was the first person to separate the thelypteroid and dryopteroid ferns, followed by Ching (1936, 1940, 1963), who proposed the family Thelypteridaceae, later validated by Pichi Sermolli (1970*a*). This was the situation at the time of publication of Copeland's *Genera Filicum* (1947), but subsequently Holttum (1947, 1949, 1968–1979), Holttum, Sen & Mittra (1970), and Holttum & Grimes (1980) have carried out much further work in separating and revising the Thelypteridaceae.

The Aspidiaceae, however, were still a large group by today's standards, containing many of the present families of the modern sub-order Aspidiineae, though some groups such as the Elaphoglossaceae and Athyriaceae were only more recently understood to be allied, the latter for example having been placed with the Aspleniaceae (see Sledge 1973*a*, though he did not recognise the athyrioid ferns as a family). Holttum (1947, 1949, 1960) gave details of the dryopteroid ferns, distinguishing them from other groups within the Aspidiaceae as the Dennstaedtiaceae subfamily Dryopteridoideae. Following the work of Ching (1940, 1965*a*, 1975), Alston (1956), and Pichi Sermolli (1968 & 1970*a*), the Aspidiaceae have today been further split so that the equivalent of the wider group is probably best treated as a suborder, the Aspidiineae, as mentioned above, consisting of nine families, the Onocleaceae Pichi-Serm. (1970*a*), Woodsiaceae (Diels) Herter (1949), Athyriaceae Alston (1956), Hypodematiaceae Ching (1975), Peranemataceae (C. Presl) Ching (1940) nom. cons. (and see Nayar & Kaur, 1966), Dryopteridaceae Ching (1965*a*), Aspidiaceae Mett. ex Frank (1877) nom. cons., Lomariopsidaceae Alston (1956) and Elaphoglossaceae Pichi-Serm. (1968); nomenclatural details of most of these are given by Pichi Sermolli (1970*b*). It should be pointed out, however, that a number of authorities prefer to treat the nine families as subfamilies of a family Aspidiaceae taken in the wide sense, in order that this should remain the equivalent of such wide families as the Aspleniaceae sens. lat., etc. Pichi Sermolli (1981) also gave details of a proposal, now accepted, to conserve the family name Aspidiaceae, which was illegitimate being based on the illegitimate name *Aspidium* Sw., a synonym of *Tectaria* Cav. The tectarioid ferns have no other family name and the name Aspidiaceae is therefore used for them in this paper (i.e. in the narrow sense).

In addition Pichi Sermolli proposed the conservation, now accepted, of the name Dryopteridaceae against the name Peranemataceae when the two are combined, and of the name Peranemataceae Ching against Peranemataceae Bütschli, giving details of its spelling which he corrects from '*Peranemaceae*', and showing that the name is illegitimate, whether used for the fern family or the algal one. Previous details concerning the name Peranemaceae are given by Pichi Sermolli (1970*b*, 1977: 451). The name Peranemataceae is accordingly used here.

Within the modern Dryopteridaceae several modern genera had at one time been included under the name *Dryopteris*, but have subsequently been separated. In particular *Stigmatopteris* was separated by Christensen (1909, 1911*b*, 1913*a*, 1938) (see also Tryon & Tryon, 1981), *Lithostegia* and *Stenolepia* by Ching (1933) and van Alderwerelt van Rosenburgh (1909), *Lastreopsis* by Ching (1938) (and see Tindale, 1957, 1965), and the large and important genus *Ctenitis* by Christensen (1911*b*, 1920, 1934) and Tardieu-Blot & Christensen (1938), followed by Ching (1938), including the often confused *Ctenitis apiciflora* (Wallich ex Mett.) Ching group now placed in *Dryopsis* (Holttum, 1984). *Nothoperanema* was separated as a subgenus by Tagawa (1938), and as a genus by Ching (1966), while two genera often considered intermediate between *Dryopteris* and *Polystichum*, but closer to the latter, have been clarified as *Arachniodes* and *Leptorumohra* (see Ching, 1934, 1938, 1962; Itô, 1935*a* and *b*, 1939; Morton, 1960; Tindale 1961*a* and *b*; Widén et al., 1976, 1978, 1981).

An account of 34 dryopteridaceous genera (from *Nothoperanema* to *Rumohra*), with the Peranemataceae and Aspidiaceae sens. str., under the name Aspidiaceae, is given by Pichi Sermolli (1977), though Holttum (1984) presents a different view. Pichi Sermolli included *Rumohra* as an aspidiaceous fern, a viewpoint which the author tentatively accepts, though it has recently been considered a davallioid fern and thus not related to *Arachniodes*, most of the species of which were once placed in *Rumohra*. The name *Arachniodes* is retained here pending further investigation to determine whether or not the type of the earlier described monotypic genus *Rumohra, R. aspidioides* Raddi (= *R. adiantiformis* (G. Forster) Ching), belongs to the same genus as *Arachniodes* species; its present separation, mainly on the basis of its markedly creeping, 'davallioid' rhizome, perhaps being artificial and incorrect; a long, creeping rhizome occurs in some *Arachniodes* species too, which deserves anatomical study (by contrast, see Holttum, 1984).

Dryopteris itself in the modern sense has close relationships with several genera and is sometimes not clearly separable from them by definition alone. This is a problem that often affects the delineation of genera or subgenera and too many authors tend to stick rigidly to certain normally characteristic features as the only way to separate species into genera, rather than allowing exceptions in order to follow a more natural arrangement which is usually more workable. These ranks are often more naturally defined by reference to the species groups within them, and the necessity for a description is often allowed to upset generic boundaries unnecessarily. Sledge (1973*a*) has pointed out that the borderline between *Dryopteris* and *Arachniodes* needs further consideration and (1973*b*) has revised several species that had been treated by Ching (1938) according to strict rules based on rigid morphological marker characteristics; much of the difficulty in the past having been caused by members of *Dryopteris* subgenus *Nephrocystis* being placed partly in *Arachniodes*. It is not difficult to make a natural division between the two genera, but nevertheless they are somewhat close, though *Arachniodes* is far more closely related to *Polystichum*, the latter being further removed from *Dryopteris*.

Arachniodes and most of the polystichoid genera share an important feature not found in *Dryopteris*: the apices of the segments and of their basal acroscopic side-lobes, when present, end in an acute point bearing a single stiff, 'cartilaginous' tooth. Although some slight exceptions occur in *Polystichum*, this appears to be a fundamental morphological distinction between the two groups, probably even more so than the presence of a peltate indusium in *Polystichum*, while there is a more or less reniform one in *Dryopteris* and *Arachniodes*. Indeed in *Arachniodes* both indusial conditions occur. *Arachniodes* and most of the species of *Polystichum* also have a markedly more stiffly coriaceous lamina and teeth in contrast to *Dryopteris*, though not surprisingly some exceptions occur and *Arachniodes* species frequently have a creeping rhizome, rare in *Dryopteris*. Members of the genus *Arachniodes* and of the genus *Dryopteris* are readily separable from each other with little difficulty, which emphasises the natural and useful division of the two genera, and the view (e.g. Tryon & Tryon, 1982*b*) that *Arachniodes* should be sunk into *Dryopteris* is certainly unjustified unless *Dryopteris*, *Arachniodes*, *Polystichum*, etc. are all combined, which would be even more impracticable. Tryon &

Tryon (1982*a* and *b*) did not correctly distinguish between polystichoid and dryopteroid ferns when placing the clearly polystichoid genus (as pointed out by Ching, 1965*b*) *Phanerophlebiopsis* Ching into their subgenus *Dryopteris* in error. Indeed, their work contains no mention of the important groups of species within the genera concerned and it should be noted that the vast majority of species of *Arachniodes* are Asiatic and cover a range of form far wider than that found in the American species more familiar to them. They also state that *Dryopteris* and *Arachniodes* combined contain only about 150 species.

Dryopteris subgenus *Nephrocystis* (including the genus *Acrorumohra*) is recognised here as representing a discrete transition group towards *Leptorumohra* and *Nothoperanema*, while the subgenus *Erythrovariae*, which may be a more primitive group than subgenus *Dryopteris*, shows some similarities in frond morphology to *Ctenitis*. Subgenus *Erythrovariae* also has some members (section *Variae*) which appear superficially to be distantly related to *Arachniodes*. Some useful information on the genus *Arachniodes*, on its chemistry, and the presence or absence of glands in some of the species nearer the borderline between it and *Dryopteris*, is to be found in Widén, Sarvela & Iwatsuki (1976), Widén, Huure, Sarvela & Iwatsuki (1978), and Widén, Mitsuta & Iwatsuki (1981), though the taxonomic position of the subgenus *Nephrocystis* is not fully brought out. Clearly the relationships between all these groups are complex and reticulate.

Classification within *Dryopteris*

Dryopteris is a large and widespread genus which, not surprisingly, displays a considerable range of form, and contains several rather distinct groups, here treated as four subgenera. Within three of the subgenera there are several sections, particularly in the subgenus *Dryopteris*. The sections are less clear-cut groups of species than the subgenera and often have obvious multidirectional relationships, though still being generally recognisable as groups. A complication that often occurs is the existence of an allopolyploid species derived from two different sections, which has to be assigned to one section or the other, usually somewhat artificially by following the definition of the section, but this does not make the sections any less valid. One of the sections, the *Remotae*, is an artificial one necessary because the ancestral diploid species of the allopolyploid species concerned belong to sections so remote from each other that the resultant species cannot be placed in one or the other section as they have a quite distinct type of 'mixed' morphology unlike either parent. The sections represent natural groups of related species and are more readily defined by means of the groups of species within them than by overall descriptions of the section, which become artificial and often slightly misleading. General descriptions are given but these are necessarily somewhat vague as each contains a wide range of form. It is emphasised that the author attaches by far the more importance to the groupings of species than the sectional descriptions.

Two previous major classifications of *Dryopteris* have been published, Itô (1935*a*, 1936*a, b, c*, 1939) and Ching (1938), neither of whom were familiar with species on a world-wide scale and whose classifications were based mainly on the species from their own species-rich study areas. Itô dealt with the dryopteroid ferns of Japan and Taiwan and (1936*a*) was the first person to separate *Erythrovariae* as a section. He also (1935*a*) separated *Nephrocystis* as a section of *Dryopteris*, though he immediately afterwards (1935*b*) recognised some species which belong to *Nephrocystis* as the section *Acrorumohra* of the genus *Rumohra* (*Arachniodes*) and later (1939) raised that section to a genus, *Acrorumohra* (H. Itô) H. Itô, which is not recognised here. He also (1939) published a superfluous name, section *Polysticho-drys*, for the *Erythrovariae*. His other sections were less meaningful and were somewhat artificially separated, though some of his subsections correspond at least partially to sections in the present treatment once discordant elements have been removed. Ching's work dealt with the Himalayan species with emphasis on some of the species from south-west China and the east Himalaya in the Indian subcontinent and with reference to additional species in the west Himalaya, south India, and Sri Lanka. It was the first treatment to deal adequately with the subgenus *Pycnopteris* and he also recognised, independently of Itô, the distinction between what he called the sections *Fibrillosae* and

Bulligerae, now the equivalent, with some modifications, of the subgenera *Dryopteris* (with its section *Fibrillosae*) and *Erythrovariae* respectively. His treatment, however, did not deal adequately with the subgenus *Nephrocystis*, some members of which he (1964), like Itô, placed in the genus *Acrorumohra*. Ching's 'groups' below his sections, though generally the equivalent of some of the present sections, often contained several discordant elements and were not clear-cut.

The present scheme attempts to place most of the world's *Dryopteris* species and distinguishes more clearly between the major groups as subgenera and the more minor ones as sections; it has involved a reappraisal of the genus world-wide and it is hoped that it is a more natural classification than has previously been produced. Species have been placed in the groups with more emphasis on natural relationships than on rigid adherence to key characteristics, which had previously caused some discordant anomalies. However, it is pertinent to point out here that the author is not as familiar with species from the neotropics, Hawaii, and the Australasian islands as with those from elsewhere. In particular, it has been necessary to obtain help with the species from the neotropical region, which has been most willingly supplied by A. R. Smith of the University of California, Berkeley, though his opinion has not been followed in its entirety. H. Hirabayashi has kindly commented on the Japanese species of subgenus *Erythrovariae*, though I have modified his comments to incorporate work on China. A synopsis of the classification is given below, the details appearing in sequence in the systematic descriptions that follow.

Dryopteris Adans.
  Subgenus 1. *Pycnopteris* (T. Moore) Ching
  Subgenus 2. *Dryopteris*
    Section 1. *Hirtipedes* Fraser-Jenkins
    Section 2. *Fibrillosae* Ching
    Section 3. *Pandae* Fraser-Jenkins
    Section 4. *Dryopteris*
    Section 5. *Remotae* Fraser-Jenkins
    Section 6. *Pallidae* Fraser-Jenkins
    Section 7. *Splendentes* Fraser-Jenkins
    Section 8. *Cinnamomeae* Fraser-Jenkins
    Section 9. *Marginatae* Fraser-Jenkins
    Section 10. *Aemulae* Fraser-Jenkins
    Section 11. *Lophodium* (Newman) C. Chr. ex H. Itô
  Subgenus 3. *Erythrovariae* (H. Itô) Fraser-Jenkins
    Section 1. *Erythrovariae*
    Section 2. *Politae* Fraser-Jenkins
    Section 3. *Variae* Fraser-Jenkins
  Subgenus 4. *Nephrocystis* (H. Itô) Fraser-Jenkins
    Section 1. *Purpurascentes* Fraser-Jenkins
    Section 2. *Nephrocystis*

Taxonomy

Dryopteris Adans., *Fam. pl.* **2**: 20, 551 (1763), nom. cons.

Psidopodium Necker, *Elem. bot.* **3**: 315 (1790) (fide Christensen, 1906: 590).
Nephrodium Rich. in Marthe, *Cat. pl. jard. méd. Paris*: 120 (1801), nom. nud. (Art. 32.1).
Nephrodium Rich. in Marthe ex Michaux, *Fl. bor.-amer.* **2**: 266 (1803). Lectotype (Pichi Sermolli 1977*b*): *Nephrodium marginale* (L.) Michaux (= *Dryopteris marginalis* (L.) A. Gray).
Arthrobotrys Wallich, *Num. List*: no. 395, 1034 (1828), nom. nud. (Art. 32.1), represented by *Arthrobotrys macrocarpa* Wallich, nom. nud. (Art. 32.1) (= *Dryopteris cochleata* (Buch.-Ham. ex D. Don) C. Chr.).
Lophodium Newman in *Phytologist* **4**: 371, app. 16 (1851). Lectotype: *Lophodium multiflorum* (Roth) Newman (= *Dryopteris dilatata* (Hoffm.) A. Gray).

Dichasium (A. Braun) Fée, *Mém. foug.* **5**: 302 (1852). Lectotype: *Aspidium patentissimum* (Wallich ex Kunze) Franchet (= *Dryopteris wallichiana* (Sprengel) N. Hylander).

Pycnopteris T. Moore in *Gdnrs' Chron.* **1855**: 468 (1855). Type: *Pycnopteris sieboldii* (Van Houtte ex Mett.) T. Moore (= *Dryopteris sieboldii* (Van Houtte ex Mett.) Kuntze).

Diclisodon T. Moore, *Index fil.*: 95 (1857). Type: *Diclisodon deparioides* T. Moore (= *Dryopteris deparioides* (T. Moore) Kuntze).

Acrorumohra (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 101 (1939 ['1938']).

Misapplied names: *Polypodium* L., *Polystichum* Roth, *Aspidium* Sw., *Lastrea* Bory, *Rumohra* Raddi, *Phegopteris* Fée, *Polystichopsis* (J. Smith) Holttum, *Arachniodes* Blume, *Byrsopteris* C. Morton.

Type: *Polypodium filix-mas* L. (= *Dryopteris filix-mas* (L.) Schott).

Rhizome normally terrestrial, more or less thick, creeping below but usually with an upright or ascendent apex, closely surrounded by spirally arranged old leaf-bases, rarely becoming elongated so that the leaf-bases are widely separated, often branching, bearing narrow scales at the apex. Fronds usually somewhat large, once to four times pinnate (rarely five times pinnate), may bear glands or hair-like scales (fibrils) but not hairs; stipe and often rachis, costae, etc. bearing scales and often densely scaly; stipe with a ring of several (more than two) separate vascular strands inside it and bearing a deep groove along its upper surface which is continuous with that on the rachis, rachis groove continuous with those on the pinna-costae; lamina herbaceous or somewhat coriaceous, may bear glands or hair-like scales (fibrils) but not hairs, arrangement of (lower) pinnulets usually but not always catadromous; costae and costules canaliculated above and arising from the rachis at a more or less acute angle, the channels being continuous between them; veins in the segments free, simple or pinnate, terminating in small but slightly enlarged vein-endings lying just inside the segment margin; segment base symmetrical or asymmetrical, but though occasionally slightly bluntly auriculate on the acroscopic side, does not bear a marked deltate and pointed auricle ending in a single long-acute or aristate tooth; segment margins frequently toothed, particularly at their apices, but the apex, though often acute, does not end in a single long-acute or aristate tooth at the tip; the teeth range from obtuse crenations to aristate or hair-pointed ones. Sori borne on either side of the pinna-, pinnule-, or ultimate segment-midribs, separate, circular, borne dorsally or rarely apically on the veins, normally indusiate; indusium attached centrally to the receptacle in the middle of the sorus, more or less large, thick or thin, persistent, or shrivelling and deciduous, rounded or cordate, with a deep, narrow sinus at one side reaching in to the point of attachment, thus becoming near to reniform in shape, margins entire or fimbriate, flat or curved down around the sorus. Spores bilateral, perisporate. Base chromosome number 41. Species often polyploid and frequently apomictic, though in the subgenus *Dryopteris* apomixis is mainly but not entirely associated with the presence of genomes from the sections *Hirtipedes* and *Fibrillosae*, or else is frequent in the subgenus *Erythrovariae*. Some further details of *Dryopteris* frond morphology are given by Serizawa (1974, 1976), including details of glands, etc.

Dryopteris is a large genus of about 225 species, though others presumably exist in complexes such as the *D. sparsa* and *D. inaequalis* groups which have yet to be elucidated, and probably also in the section *Cinnamomeae* in the neotropics (Smith, 1981 pers. comm.), and doubtless in other groups elsewhere. They largely occupy the forest or sometimes rocky and alpine zones of northern temperate or sub-temperate latitudes, or otherwise subtropical and tropical montane regions. Some species also occur in southern temperate regions, having either spread from the north, or with their nearest relatives in the north. Copeland (1947) has suggested a southern origin for all the modern fern genera, but though this could conceivably be possible for *Dryopteris*, there is no clear evidence. Its centre of distribution and diversity is in south-west China and the east Himalaya, with another centre about Japan (including south-east and south China) and centres of secondary importance in Taiwan, the west Himalaya, south-east Asia and the Australasian/Pacific islands, south India and Sri Lanka, East Africa and Madagascar, Europe (including Macaronesia, west Asia and west and central Siberia), eastern North America and finally Central America and western South America. Species of *Dryopteris* are present in all the continents except Antarctica, though they become scarce in Australasia and

Oceania (17 species) and only one species occurs naturally in mainland Australia, being a south-east Asian element (two extra species are introduced in New Zealand).

The approximate numbers of species from different areas are given below, though it should be noted that only in North America, Europe (in the wide sense), Japan, and the Indian subcontinent has the genus been carefully elucidated according to modern systematic principles. However, the author has been able to make a preliminary study of species from China in Chinese and European herbaria. It should be noted that the figures for endemic species are not so meaningful from the areas in Asia mentioned below as they would be if the natural floristic areas were to be considered, for example, south and south-west China combined with the Indo-Himalaya forms one floristic area, and Japan with east China forms another. If the numbers from the natural floristic areas are considered, the numbers of endemic species increase markedly. North America (U.S.A. and Canada): 16 species (6 endemic). Central and South America (including Easter Island): 15 species (1 introduced, 10 endemic). South Atlantic islands: 4 species (3 endemic). Europe (sens. lat., including north-west Africa, Cape Verde Islands, Macaronesia, western Asia (to Iran), Soviet central Asia and Siberia, east to Irkutsk): 26 species (18 endemic). Africa (including Madagascar, Mascarenes, Seychelles, and south Indian Ocean islands but excluding north-west Africa): 22 species (21 endemic). South Arabia: 1 species (0 endemic). Indian subcontinent: 57 species (13 endemic). China (excluding Taiwan), Tibet, and Mongolia: 103 species (18 endemic). Taiwan: 40 species (3 endemic). Korea: 27 species (3 endemic). Japan: 59 species (12 endemic). Far east Siberia: 8 species (0 endemic). South-east Asia (including the Philippines but excluding Burma): 31 species (1 endemic). Burma: unknown. Australasian and Pacific isles (excluding Hawaii, South America, and Easter Island): 20 species (9 endemic). Australian mainland and New Zealand: 3 species (2 introduced, 0 endemic). Hawaii: 10 species (9 endemic).

Subgenus 1. Pycnopteris (T. Moore) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8**: 365–396 (1938).

Pycnopteris T. Moore in *Gdnrs' Chron.* **1855**: 468 (1855).
Dryopteris group *Pycnopteris* (T. Moore) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).
Dryopteris section *Eudryopteris* subsection *Pycnopteris* (T. Moore) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 25 (1939 ['1938']).

Type: *Pycnopteris sieboldii* T. Moore (= *Dryopteris sieboldii* (Van Houtte ex Mett.) Kuntze).

Morphology as in subgenus *Dryopteris* except for the fronds being imparipinnate (i.e. with the frond apex ending in a segment similar to one of the lateral pinnae), and only once pinnate, not becoming nearly bipinnatifid, though the pinnae may be shallowly and irregularly lobed. All the species have fronds of a hard-coriaceous texture, harder than those of the other subgenera. One species is exindusiate.

Contains *c.* four species, confined to eastern Asia: *D. sieboldii* (Van Houtte ex Mett.) Kuntze, *D. pseudosieboldii* Hayata, *D. bodinieri* (Christ) C. Chr., and *D. podophylla* (Hook.) Kuntze*.

Subgenus 2. Dryopteris

Lastrea subgenus *Arthrobotrys* Wallich ex C. Presl, *Tent. pterid.*: 77 (1836).
Dryopteris subgenus *Eudryopteris* C. Chr., *Index filic.*: 250 (1905), nom. inval. (Art. 21.3).
Dryopteris subgenus *Eudryopteris* C. Chr., *Biol. Arbejd. tileg. Eug. Warming*: 76 (1911), nom. inval. (Art. 21.3).

Type: *Polypodium filix-mas* L. (= *Dryopteris filix-mas* (L.) Schott).

Fronds varying from once to nearly four times pinnate, not imparipinnate, but pinnae gradually reduced to a pinnatifid apex. Stipe and rachis well supplied with scales which are often present

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* The species listed are arranged in a taxonomic order, normally from the least to the most dissect, but taking account of closely related groups. A question-mark (?) denotes a species of doubtful status, requiring further investigation or confirmation.

on the pinna-costae too, at least some scales near the stipe base somewhat wide; scales on the underside of the pinna-costae (as elsewhere) not bullate; lamina coriaceous or lax, but not hard-coriaceous; pinna segments usually more or less symmetrical about their axes and not sloping or auriculate at their acroscopic bases except in a few cases (mostly in the sections *Splendentes* and *Cinnamomeae* with a few examples in the *Pallidae* and *Marginatae*).

Throughout the range of the genus and the only subgenus present in Europe and most of North and South America and Africa.

Section 1. **Hirtipedes** Fraser-Jenkins, **sect. nov.**

Dryopteris section *Eudryopteris* subsection *Cycadinae* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 19 (1939 ['1938']).

Frondes unipinnatae, sed pinnis usque ad medium saepe lobatis.

Type: *Dryopteris hirtipes* (Blume) Kuntze.

Morphology as in section *Dryopteris* except for the fronds being only once pinnate and the pinnae only shallowly lobed or lobed up to half their depth on each side; rarely the lowest basiscopic pinna-lobe of the lowest pinnae may become fully separated. Stipe scales narrower than in section *Dryopteris* and, like those of section *Fibrillosae*, usually mostly linear-lanceolate. Several of the species are apomictic. This section is probably distantly related to subgenus *Pycnopteris* and is similar in having shallowly lobed pinnae, though the lobes are somewhat more regular in section *Hirtipedes*; it also shows clear similarities to section *Fibrillosae* and some similarities to the simply pinnate members of subgenus *Erythrovariae*. Two species are exindusiate.

Contains *c.* 17 species confined to south and eastern Asia and the Australasian and Pacific isles: *D. liankwangensis* Ching, *D. scottii* (Beddome) Ching, *D. hirtipes* (Blume) Kuntze and subspp., ? *D. fatuhivensis* E. Brown, *D. commixta* Tag., *D. darjeelingensis* Fraser-Jenkins in press, *D. cycadina* (Franchet & P. A. L. Savat.) C. Chr., *D. hangchowensis* Ching, *D. stenolepis* (Baker) C. Chr., *D. handeliana* C. Chr., *D. namegatae* Kurata, *D. dickinsii* (Franchet & P. A. L. Savat.) C. Chr., *D. pycnopteroides* (Christ) C. Chr., *D. subpycnopteroides* Ching ex Fraser-Jenkins, *D. microlepis* (Baker) Ching, *D. lunanensis* (Christ) C. Chr., and *D. conjugata* Ching.

Section 2. **Fibrillosae** Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8**: 366 (1938).

Aspidium subgenus *Dichasium* A. Braun in *Flora, Jena* **24**: 710 (1841).
Dichasium (A. Braun) Fée, *Mém. foug.* **5**: 302 (1852).
Dryopteris section *Eudryopteris* subsection *Dichasium* (A. Braun) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 6 (1939 ['1938']).

Type: *Dryopteris fibrillosa* (C. B. Clarke) Hand.-Mazz., non (Baker) C. Chr. (= *D. pulcherrima* Ching).

Morphology exactly as in section *Hirtipedes* except for the pinnae being very nearly twice pinnate as the pinna-lobes are cut down nearly to the pinna-costa, leaving them connected only by a very narrow wing of tissue. Some of those at the bases of the lowest few pairs of pinnae may become fully separated into pinnules. Similar to section *Dryopteris* in the fronds being more or less linear-lanceolate, though slightly narrower at the base, but the pinna-lobes are normally markedly regular, parallel-sided, and untoothed at the sides and are either unlobed or more or less shallowly lobed, the side-lobes being rectangular; the lobe-apices have a far more marked tendency to be truncate or rounded-truncate and bear shorter teeth. Differs from section *Dryopteris* in having the lamina more or less coriaceous, somewhat dark-green (often yellowish or pinkish when young) and glossy above, and the stipe and rachis more densely clothed with narrowly lanceolate scales; dense hair-like scales (fibrillae) are also present on the rachis and are often present on the lamina. The indusia are thicker and turned down or inflected at the edges, at least in the early stages, and are more persistent. Most of the species are apomictic.

Members of this section were previously often referred to the *D. filix-mas* group as a result of early European botanists not distinguishing *D. affinis* (in the present section) from *D. filix-mas*, but it is a markedly distinct section, probably related to the section *Hirtipedes*.

Contains *c.* 21 species, throughout most of the range of the genus except for North America, rare in Africa and only one introduced species in Australasia (New Zealand). Many of the species are apparently derived from *D. wallichiana* or its relatives by hybridisation with a sexual diploid species to form a new species (see also section *Remotae*). Being apomictic, several of the species are markedly variable and may have been divided into unwarranted species by various authors, but it is also possible that further new species may yet be recognised that are at present included in other species. To the section belong *D. parrisiae* Fraser-Jenkins, *D. pulcherrima* Ching., *D. polylepis* (Franchet & P. A. L. Savat.) C. Chr., *D. crassirhizoma* Nakai and subsp. **whangshangensis** (Ching) Fraser-Jenkins **comb. nov.** (basionym: *Dryopteris whangshangensis* Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8**: 421 (1938)), *D. neorosthornii* Ching, *D. redactopinnata* Panigr. & S. K. Basu, *D. rosthornii* (Diels) C. Chr., *D. yigongensis* Ching, *D. acuto-dentata* Ching, *D. incisolobata* Ching & S. K. Wu, *D. wallichiana* (Sprengel) N. Hylander, **D. reichsteinii** Fraser-Jenkins **nom. et stat. nov.** (*D. paleacea* var. *madagascariensis* C. Chr. in *Dansk bot. Ark.* **7**: 53 [1932]; type: Madagascar, Mt Tsaratanana, 2400 m, April 1924, *Perrier* 16454 [P!]), *D. chrysocarpa* (Fée) Rothm., *D. affinis* (Lowe) Fraser-Jenkins and subspp., *D. madrasensis* Fraser-Jenkins in press, *D. fusco-atra* (Hillebrand) W. Robinson, *D. lepidopoda* Hayata, *D. sledgei* Fraser-Jenkins in press, *D. pseudo-filix-mas* (Fée) Rothm., *D. khullarii* Fraser-Jenkins in press, and *D. hawaiiensis* (Hillebrand) W. Robinson.

Section 3. Pandae Fraser-Jenkins, sect. nov.

Lastrea subgenus *Arthrobotrys* Wallich ex C. Presl, *Tent. pterid.*: 77 (1836).

Frondes unipinnatae vel bipinnatae; pinnae herbaceae, haud nitidae, marginibus loborum non parallelis. Stipes non dense paleaceus.

Type: *Dryopteris panda* (C. B. Clarke) Christ.

Similar to section *Dryopteris* in having more or less linear-lanceolate or lanceolate fronds which are once pinnate, but become twice pinnate as the pinna-lobes may be cut down very nearly to the pinna-costa; some of those at the bases of the pinnae may become fully separated into pinnules, but the connecting wing of tissue between pinnules, when present, is usually slightly wider. As in section *Dryopteris* the lobes or pinnules are only slightly, not markedly, parallel-sided and are either unlobed or more or less shallowly lobed, with side-lobes (when present) not markedly rectangular, in contrast to section *Fibrillosae*. Lamina either thin as in section *Dryopteris*, or somewhat thickly herbaceous and almost very slightly succulent and easily snapped, not coriaceous in texture; pale-green and not glossy above, in contrast to section *Fibrillosae*. Stipe and rachis usually less densely clothed in scales than in sections *Fibrillosae* and *Dryopteris* and lamina more or less devoid of scales or with only a very few. Sori in most species markedly larger than in other sections, with a thick or thin, usually tall indusium which is usually (but not always) curved down at the sides and in some species is inflected and may not lift even on sporangial maturity. Spores often larger than in other sections (at the diploid level) and often uniquely reddish or chestnut brown under the light microscope.

Contains *c.* 17 species, throughout the range of the genus in the northern hemisphere: *D. ludoviciana* (Kunze) Small, *D. tokyoensis* (Matsum. & Makino) C. Chr., *D. habaensis* Ching, *D. panda* (C. B. Clarke) Christ, *D. bonatiana* (Brause) Fraser-Jenkins in press, *D. costalisora* Tag., *D. woodsiisora* Hayata, *D. austro-indica* Fraser-Jenkins in press, *D. chrysocoma* (Christ) C. Chr., ? *D. para-chrysocoma* Ching & Z. R. Wang in press, *D. fangii* Ching, Fraser-Jenkins & Z. R. Wang in press, *D. zinongii* Z. R. Wang & Fraser-Jenkins in press, *D. himachalensis* Fraser-Jenkins in press, *D. nobilis* Ching, *D. cristata* (L.) A. Gray, *D. clintoniana* (D. Eaton) Dowell, and *D. celsa* (W. Palmer) Small.

Section 4. Dryopteris

Aspidium group *Filix-mas* Christ, *Farnkr. Erde*: 256 (1897), nom. nud. (Art. 32.1).
Aspidium group *Fragrantia* Christ, *Farnkr. Erde*: 260 (1897), nom. nud. (Art. 32.1).

Dryopteris group *Filix mas* C. Chr., *Index filic.*: XXI (1905), nom. nud. (Art. 32.1).

Dryopteris section *Eudryopteris* (C. Chr.) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 5 (1939['1938']), nom. inval. (Art. 21.3).

Dryopteris section *Eudryopteris* subsection *Monticolarum* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 23 (1939 ['1938']).

Dryopteris section *Lophodium* subsection *Fragrantes* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 71 (1939 ['1938']).

Type: *Dryopteris filix-mas* (L.) Schott.

Fronds linear-lanceolate to lanceolate, twice pinnate, the pinnules widely attached to the costae except at the bases of the lower pinnae. Pinnules slightly but not markedly parallel-sided, usually somewhat tapering to their apices from about two-thirds of their length, toothed at the sides and markedly so at their apices, with long acute teeth, usually shallowly lobed with pointed side-lobes. Lamina matt and herbaceous, neither coriaceous nor glossy, stipe and rachis sparsely or somewhat densely clothed with scales, scales mostly lanceolate or ovate-lanceolate, though narrow ones also occur, including hair-like ones (fibrils) on the lamina in some species. Sori indusiate, with a thin or somewhat thick indusium which is flat or curved down at the edges, lifting and shrivelling on ripening. Several species are somewhat densely glandular on the costae.

Contains *c.* 15 species, throughout the range of the genus but absent from south-east Asia and Australasia (apart from *D. filix-mas* introduced in New Zealand) and most of Africa and South America: *D. sichotensis* V. Komarov*, *D. oreades* Fomin, *D. fragrans* (L.) Schott, *D. barbigera* (T. Moore ex Hook.) Kuntze and subspp., *D. tingiensis* Ching & S. K. Wu ex Fraser-Jenkins, *D. alpestris* Tag., *D. serrato-dentata* (Beddome) Hayata, *D. villarii* (Bellardi) Woynar ex Schinz & Thell., *D. mindshelkensis* Pavlov†, *D. tyrrhena* Fraser-Jenkins & Reichst., *D. ardechensis* Fraser-Jenkins, *D. filix-mas* (L.) Schott, *D. caucasica* (A. Braun) Fraser-Jenkins & Corley, *D. montigena* Ching, and *D. goldiana* (Hook.) A. Gray and subsp. **monticola** (Makino) Fraser-Jenkins **comb. nov.** (basionym: *Nephrodium monticola* Makino in *Bot. Mag., Tokyo* **13**: 80 (1899)).

Section 5. **Remotae** Fraser-Jenkins, **sect. nov.**

Frondes bipinnatae, anguste lanceolatae; stipes rhachisque aliquantum dense paleacei. Pinnulae in parte inferiora frondis profunde lobatae sed in parte superiora fere non lobatae; lobi rectangulari.

Type: *Dryopteris remota* (A. Braun ex Doell) Druce.

Similar to section *Dryopteris* except that the fronds are lanceolate to very narrowly triangular-lanceolate (i.e. wider at the base), and the pinnules are more narrowly attached to the costa at the bases of the pinnae and are markedly more deeply lobed in the lower part of the frond. The pinnule-lobes are rectangular and the indusia somewhat thick as in section *Fibrillosae*.

This section contains presumed allopolyploid species whose presumed origin is by hybridisation between species from such widely different sections (e.g. *Fibrillosae* and *Lophodium* or *Marginatae*) that their morphology does not fit in any section and they have had to be referred to an artificial section of their own.

Contains *c.* three species, in Europe and the Sino-Himalayan region: *D. remota* (A. Braun ex Doell) Druce, non Hayata, *D. blanfordii* (C. Hope) C. Chr. and subspp., and *D. corleyi* Fraser-Jenkins.

Section 6. **Pallidae** Fraser-Jenkins, **sect. nov.**

Frondes anguste triangulari-lanceolatae, bipinnatae. Pinnulae in dimidio inferiore pinnae stipitatae, in parte superiore adnatae.

Type: *Dryopteris pallida* (Bory) C. Chr. ex Maire & Petitm.

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* Formerly considered by Fraser-Jenkins & Corley (1973) to be synonymous with *Dryopteris oreades* (under the names *D. coreano-montana* Nakai and *D. abbreviata* (DC.) Newman), but now reinstated as a distinct species related to *D. oreades*.

† Formerly reduced by Fraser-Jenkins (*Candollea* **32**: 305–319 (1977)) to a subspecies of *D. villarii*, but now reinstated as a species close to the latter.

Similar to section *Dryopteris* except that the fronds are markedly wider at their bases, being ± narrowly triangular-lanceolate, and the pinnules are stalked, or with narrow bases up to about half way up the pinna and are more or less parallel-sided with rounded or more pointed apices, usually bearing somewhat wider-based acute teeth, lobed or unlobed at the sides. Lamina often slightly more crispaceous. The stipe is much longer and well-clothed with more ovate-lanceolate and more glossy scales, scaly only at the base, scales usually becoming more scattered than in section *Dryopteris* or absent further up, and with very much fewer or no fibrillae. Indusia small but slightly thicker than in section *Dryopteris*, usually curved down at the edges, but not tightly enclosing the sorus. As in section *Dryopteris* several species are somewhat densely glandular on the costae. Several of the species are apomictic.

Contains *c.* 17 species, throughout the range of the genus except South America, Africa (but present in western North Africa), south-east Asia, Australasia, north Europe and north Asia: *D. marginalis* (L.) A. Gray, *D. sericea* C. Chr., *D. peninsulae* Kitagawa, *D. lacera* (Thunb.) Kuntze, *D. uniformis* (Makino) Makino, *D. sublacera* Christ, *D. basisora* Christ, *D. odontoloma* (Beddome) C. Chr., *D. juxtaposita* Christ, *D. nigropaleacea* (Fraser-Jenkins) Fraser-Jenkins, *D. pallida* (Bory) C. Chr. ex Maire & Petitm. and subspp., *D. submontana* (Fraser-Jenkins & Jermy) Fraser-Jenkins, *D. arguta* (Kaulf.) Watt, *D. aitoniana* Pichi-Serm., *D. stewartii* Fraser-Jenkins, *D. lachoongensis* (Beddome) Nayar & Kaur, and *D. fructuosa* (Christ) C. Chr.

Section 7. Splendentes Fraser-Jenkins, **sect. nov.**

Frondes bipinnatae vel in una specie fere tripinnatae, lanceolatae vel elongate triangulari-lanceolatae. Pinnulae praeter in partem superiorem pinnae ad costam anguste affixae, basi valde asymmetricae, latere acroscopico quam latere basiscopico longiori, sed basi acroscopica non auriculata.

Type: *Dryopteris splendens* (Hook.) Kuntze.

Similar to section *Pallidae* except that the fronds are generally longer, elongated triangular-lanceolate, but still with a wide base, and in one species nearly tripinnate. The pinnules are distinct in being markedly asymmetrical at their bases with the lobes on the acroscopic side longer and larger than the more obliquely sloping and narrow ones on the basiscopic side, but not auriculate at the acroscopic base (as in *Polystichum*). The stipe is usually thicker and often dark-coloured. In its remarkable asymmetric pinnules this section shows a similarity to subgenus *Nephrocystis*, but in other features it is clearly more like subgenus *Dryopteris* and in particular section *Pallidae*.

Contains *c.* six species, confined to the east Himalaya, China including Taiwan, and New Guinea: *D. bamleriana* Rosenstock, *D. splendens* (Hook.) Kuntze, *D. kwanzanensis* Tag., *D. reflexosquamata* Hayata, *D. rubripes* Ching & Chu in prep., and *D. sikkimemsis* (Beddome) Kuntze.

Section 8. Cinnamomeae Fraser-Jenkins, **sect. nov.**

Frondes unipinnatae (sed fere bipinnatae) vel bipinnatae vel fere tripinnatae. Pinnulae valde devexae, non lobatae vel profunde lobatae vel pinnatisectae; lobi pinnularum basi inaequilateri, latere acroscopica quam basiscopica plerumque leviter longiori.

Type: *Dryopteris cinnamomea* (Cav.) C. Chr.

Fronds varying from once pinnate (but nearly bipinnate) to bipinnate or nearly tripinnate and from lanceolate to narrowly triangular-lanceolate. Differs from the other sections in the lamina usually being more thinly herbaceous and brittle, and in the pinnules markedly obliquely sloping and often somewhat narrowed to their bases. Pinnule-lobes, when present, somewhat similar, but not as extreme as in section *Splendentes*, in being narrow and usually slightly longer at the base of the acroscopic side of the pinnule than at the base of the basiscopic side. Indusia thin, but tall and curved down at the edges as in many species of section *Pandae*. Several species are markedly glandular. This section contains a group of species of rather wide morphological diversity in the degree of pinnation and dissection, but they appear to form a distinct natural group connected by their sloping pinnules, usually with narrower bases, and are perhaps not particularly closely related to the other sections.

Contains *c.* 12 species, mainly in South and Central America with two species reaching southern California and another reaching Easter Island; three species are also present in Africa. To the section belong *D. saffordii* C. Chr., *D. cinnamomea* (Cav.) C. Chr., *D. patula* (Sw.) L. Underw., *D. glandulifera* (Liebm.) C. Chr., *D. huberi* (Christ) C. Chr., *D. schnellii* Tard., *D. munchii* A. Reid Smith, *D. mexicana* (C. Presl) C. Chr., *D. maxonii* L. Underw. & C. Chr., *D. athamantica* (Kunze) Kuntze, *D. esterhuyseniae* Schelpe & N. C. Anthony, and *D. karwinskyana* (Mett.) Kuntze. Information about the species has been taken partly from Christensen (1911*a* & 1913*a*), A. R. Smith (1981 pers. comm.), and from preliminary study by the present author.

Section 9. Marginatae Fraser-Jenkins, **sect. nov.**

Frondes magnae, bipinnatae vel plerumque tripinnatae interdum quadripinnatae, plerumque late triangulariter lanceolatae; dentes segmentorum acumen capillaceum aristatum haud ferentes.

Type: *Dryopteris marginata* (Wallich ex C. B. Clarke) Christ.

Differs from section *Dryopteris* in its usually large fronds which range from bipinnate to, more normally, tripinnate or sometimes four times pinnate, with the pinnules and often pinnulets mostly stalked or narrowly attached except in the upper parts of the pinnae. The fronds differ markedly in their usually widely triangular-lanceolate shape, and unlike most species of other sections often arise from a prostrate or creeping rhizome; the ultimate segments are somewhat distant and, unlike section *Lophodium*, do not bear aristate hair-points. As in section *Dryopteris* the lamina is mid-green, herbaceous, and matt, but it differs markedly in having a long stipe, often as long as the lamina (as in section *Pallidae*), clothed with scattered, thin, usually matt, ovate-lanceolate scales. The indusia (as in section *Dryopteris*) are small, thin, slightly curved down at the edges and lift and shrivel on ripening except in two species which are exindusiate (*D. ruwenzoriensis* and *D. chaerophyllifolia*). The spores are similar to section *Dryopteris* and are not minutely spinulose as in section *Lophodium*, with which this section might sometimes be confused, except that one species has bluntly echinate spores (*D. ruwenzoriensis*). A few of the species are apomictic.

Contains *c.* 26 species, throughout southern and eastern Asia and Africa, with one species reaching Yemen: *D. cochleata* (Buch.-Ham. ex D. Don) C. Chr., *D. pteridiiformis* Christ, *D. angustifrons* (T. Moore ex Hook.) Kuntze, *D. subimpressa* Loyal, *D. schimperiana* (Hochst. ex A. Braun) C. Chr., *D. ruwenzoriensis* C. Chr., *D. approximata* Sledge, *D. pentheri* (Krasser) C. Chr., *D. fadenii* Pichi-Serm., *D. lewalleana* Pichi-Serm., *D. dracomontana* Schelpe & N. C. Anthony, *D. inaequalis* (Schldl.) Kuntze, *D. goeringiana* (Kunze) Koidz., *D. ramosa* (C. Hope) C. Chr., *D. shiroumensis* Kurata & Nakaike, *D. bojeri* (Baker) Kuntze, *D. oligodonta* (Desv.) Pichi-Serm., *D. caroli-hopei* Fraser-Jenkins in press, *D. marginata* (Wallich ex C. B. Clarke) Christ, *D. subarborea* (Baker) C. Chr., *D. chaerophyllifolia* (Zipp.) C. Chr., *D. aquilinoides* (Desv.) C. Chr., *D. porosa* Ching, *D. mangindranensis* Tard., *D. manniana* (Hook) C. Chr., and ? *D. manniana* auct. [S. and E. Africa].

Section 10. Aemulae Fraser-Jenkins, **sect. nov.**

Frondes tripinnatae, deltatae vel deltato-lanceolatae; dentes segmentorum acumen capillaceum aristatum ferentes. Sporae spinulis minutis haud munitae.

Type: *Dryopteris aemula* (Aiton) Kuntze.

Similar to section *Lophodium* but with lanceolate (not ovate-lanceolate), matt, concolorous stipe-base scales, more deltate or widely triangular-lanceolate fronds and the spores not minutely spinulose.

Species of this section are intermediate in morphology between the sections *Pallidae* and *Lophodium*.

Contains *c.* three species in Europe and far eastern Asia: *D. chinensis* (Baker) Koidz., *D. gymnophylla* (Baker) C. Chr., and *D. aemula* (Aiton) Kuntze.

Section 11. Lophodium (Newman) C. Chr. ex H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 65 (1939 ['1938']).

Lophodium Newman in *Phytologist* **4**: 371, appendix XVI (1851).
Aspidium group *Spinulosa* Christ, *Farnkr. Erde*: 261 (1897), nom. nud. (Art. 32.1).
Dryopteris group *Lophodium* (Newman) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).

Lectotype: *Lophodium multiflorum* (Roth) Newman (= *Dryopteris dilatata* (Hoffm.) A. Gray). Christensen (1905: XXI) selected *D. spinulosa* auct. as the type, which was included within *L. multiflorum* by Newman. The type mentioned by Tryon & Tryon (1982*b*) was *L. foenisecii* (Lowe) Newman (= *D. aemula* (Aiton) Kuntze), but this was not included by Newman in his first circumscription of his genus (p. 371).

Similar to section *Marginatae* but with the stipe-base scales usually thicker and more glossy and usually bicoloured; the lobes of the ultimate segments are usually narrower and more pointed and they end in long hair-pointed aristate teeth (as in *Polystichum*) which are slightly longer than those in section *Aemulae*. The spores are (apparently) unique in being minutely spinulose on the surface of the perispore.

Contains *c.* 10 species, throughout the north temperate zones of the world and in Macaronesia and Africa (also one species, *D. dilatata*, introduced in the Falkland Islands): *D. carthusiana* (Villars) H. P. Fuchs, *D. antarctica* (Baker) C. Chr., *D. guanchica* Gibby & Jermy, *D. crispifolia* Rasbach, Reichst. & Vida, *D. intermedia* (Muhlenb. ex Willd.) A. Gray and subspp., *D. azorica* (Christ) Alston, *D. campyloptera* (Kunze) Clarkson, *D. dilatata* (Hoffm.) A. Gray, *D. expansa* (C. Presl) Fraser-Jenkins & Jermy, and *D. amurensis* Christ.

Subgenus 3. Erythrovariae (H. Itô) Fraser-Jenkins, **stat. nov.**

Dryopteris section *Erythro-variæ* H. Itô in *Bot. Mag., Tokyo* **50**: 32 (1936).
Dryopteris section *Polysticho-drys* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 36 (1939 ['1938']).

Type (lectotype, H. Itô (1939)): *Dryopteris erythrosora* (D. Eaton) Kuntze.

Fronds once to nearly four times pinnate and similar to subgenus *Dryopteris* except that the stipe-base usually bears a tuft of distinctive, stiff, narrow scales and the rest of the stipe in most species is more or less devoid of scales, those present usually being very narrow and more or less stiff, but a few species have the stipe clothed with wider scales throughout its length. It differs markedly in having almost all the species with very small bullate, or bullate-based scales, often appearing to be almost saccate, on the underside of the pinna-costae and often on the underside of the tip of the rachis and the pinnule-centres as well. The pinnules may be symmetrical as in subgenus *Dryopteris*, but are more usually asymmetrical about their axes and often sloping and slightly auriculate at their acroscopic bases. The lamina is usually more brittle than in subgenus *Dryopteris*. Most of the species are apomictic.

This subgenus shows some similarities to all the other subgenera and also, though more distantly, to *Nothoperanema, Ctenitis*, and *Arachniodes*; in view of this, and its wide range of form, it is possible that it could be the most primitive subgenus in *Dryopteris*. A few species (*D. assamensis, D. cyclopeltidiformis, D. integriloba* (some south-east Asian specimens), *D. polita*, and *D. yenpingensis*) usually or always do not have any bullate scales, which has caused some confusion as they are in all other respects clearly members of subgenus *Erythrovariae* and cannot be placed in subgenus *Dryopteris*. This subgenus is confined to eastern Asia, with one species in New Guinea, the main centre of distribution being in Japan and east China (including Taiwan), extending to west China, Korea, south-east Asia, and north-east India. The species do not grow at high altitudes. The present author has not studied the Japanese and Korean species of the subgenus in as much detail as most of the other species in this account, and in drawing up the lists below has relied considerably on the following authors, none of whom have worked diagnostically on the subgenus throughout Asia: Itô in Nakai & Honda (1939), Nakai (1952), Hirabayashi (1974, 1982 pers. comm.), and Nakaike (1975). However, a full assessment of Chinese and Japanese species of the subgenus has not yet been carried out, and only the more obvious cases are integrated here, following the author's work in Peking.

Section 1. Erythrovariae

Dryopteris section *Bulligerae* Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8**: 366, 371 and 475 (1938).

Dryopteris section *Polysticho-drys* subsection *Erythro-variae* (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 37 (1939 ['1938']).

Dryopteris section *Polysticho-drys* subsection *Gymnosorae* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 64 (1939 ['1938']).

Type (lectotype, H. Itô (1939)): *Dryopteris erythrosora* (D. Eaton) Kuntze.

Fronds with a herbaceous or somewhat coriaceous lamina, but not markedly stiffly coriaceous. Pinnules without caudate apices and lobes normally rounded and not pointed. Stipe scales wide or narrow; costae and costules with (or occasionally without) bullate scales below.

Contains *c*. 25 species, throughout the range of the subgenus, as follows: *D. cyclopeltidiformis* C. Chr., *D. decipiens* (Hook.) Kuntze, *D. cordipinna* Ching & Shing, *D. fuscipes* C. Chr., *D. assamensis* (C. Hope) C. Chr. & Ching, *D. purpurella* Tag., *D. integriloba* C. Chr., *D. yenpingensis* C. Chr. & Ching ex Ching, *D. championii* (Benth.) C. Chr., *D. kinkiensis* Koidz. ex Tag., *D. kenzoi* Kurata, *D. tsugiwoi* Kurata, *D. koidzumiana* Tag., ? *D. liyangensis* Ching & Lan, *D. erythrosora* (D. Eaton) Kuntze, ? *D. caudipinna* Nakai, *D. kinokuniensis* Kurata, *D. hondoensis* Koidz., *D. cystolepidota* (Miq.) Makino, *D. ryo-itoana* Kurata, *D. tenuicula* C. Matthew & Christ, *D. simasakii* (H. Itô) Kurata, *D. tenuipes* (Rosenstock) Seriz., *D. subtriangularis* (C. Hope) C. Chr., and *D. gymnosora* (Makino) C. Chr.

Section 2. Politae Fraser-Jenkins, sect. nov.

Stipes longissimus paleas paucas basi ferens, super glaber. Frondes glabrae; pinnae longe stipitatae; pinnulae valde asymmetricae, infimae basiscopicae prolongatae.

Type: *Dryopteris polita* Rosenstock.

Differs from section *Erythrovariae* in being completely glabrous and without any scales except for a tuft of narrow ones at the very base; lowest pinnae with long stalks and pinnules markedly sloping and asymmetrical, the lowest one extended.

In some respects intermediate between the subgenera *Erythrovariae* and *Nephrocystis*; the lack of bullate scales has caused its only species to be referred to *Nephrocystis* (Itô in Nakai & Honda, 1939), sub *D. laurisilvicola* T. Suzuki, but bullate scales are absent in a few other members of subgenus *Erythrovariae*, and the frond morphology is closer to subgenus *Erythrovariae* than to subgenus *Nephrocystis*.

Contains a single, somewhat isolated species distributed in south-east Asia, the Australasian islands, south China including Taiwan, and south Japan: *D. polita* Rosenstock.

Section 3. Variae Fraser-Jenkins, sect. nov.

Dryopteris section *Polysticho-drys* subsection *Formosanae* H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 62 (1939 ['1938']).

Stipes paleas angustas ferens, costis costulisque paleas bullatas ferentibus. Lamina rigide coriacea; pinnulae apice caudatae lobis acutis.

Type: *Dryopteris varia* (L.) Kuntze.

Differs from section *Erythrovariae* in the fronds having a stiffly coriaceous lamina and the pinnules with caudate apices and pointed lobes; the lowest pinnule on the lowest pinna considerably longer than the rest, as in section *Politae*, but not as dissect as in that section. Stipe scales all narrow and the costae and costules with slightly bullate-based scales in contrast to the more bullate scales of section *Erythrovariae*.

Contains *c.* 10 species, in north-east India, China including Taiwan, Japan, Korea, and the northern parts of south-east Asia, as follows: *D. saxifraga* H. Itô, *D. bissetiana* (Baker) C. Chr., *D. varia* (L.) Kuntze, *D. pacifica* (Nakai) Tag., *D. sacrosancta* Koidz., *D. hadanoi* Kurata, *D. shibipedis* Kurata, *D. insularis* Kodama, *D. sordidipes* Tag., and *D. formosana* (Christ) C. Chr.

Subgenus 4. Nephrocystis (H. Itô) Fraser-Jenkins, **stat. nov.**

Dryopteris section *Nephrocystis* H. Itô in *Bot. Mag., Tokyo* **49**: 437 (July 1935).
Aspidium group *Diclisodon* (T. Moore) Christ, *Farnkr. Erde*: 262 (1897) (Art. 35.2).
Aspidium group *Sparsa* Christ, *Farnkr. Erde*: 262 (1897), nom. nud. (Art. 32.1).
Dryopteris group *Diclisodon* (T. Moore) C. Chr., *Index filic.*: XXI (1905) (Art. 35.2).

Type: *Dryopteris hayatae* Tag. (= *D. subexaltata* (Christ) C. Chr.).

Fronds twice to four times pinnate and similar to subgenus *Dryopteris* except that they are always ± wide at the base and the stipe is long and smooth and bears fewer scales which are narrow to ovate and partly deciduous unlike subgenus *Dryopteris*; the upper stipe, rachis, and costae are glabrous or bear a few very small and very narrow scales, but do not bear bullate scales as in subgenus *Erythrovariae*. The arrangement of the pinnules or pinnulets at the base of the lamina is either catadromous as in subgenus *Dryopteris* or anadromous as in *Arachniodes*. Pinnules or pinnulets always asymmetrical and sloping, with their acroscopic sides developed, especially at their base where they often become slightly auriculate with a rounded auricle, but not as developed as in *Arachniodes* and not pointed; in subgenus *Dryopteris* only two sections have asymmetrical sloping pinnules. The lamina is usually markedly smoother and more glabrous than in subgenus *Dryopteris*.

This subgenus has been considerably confused as the arrangement of the segments can be either anadromous or catadromous; when anadromous, the species have often been placed in the genus *Arachniodes* or in the separate genus, *Acrorumohra*, disregarding their close natural relationships to other species placed in *Dryopteris*. Thus Itô (1935*a* and *b*) placed some of the species in *Dryopteris* section *Nephrocystis* and some in *Rumohra* (i.e. *Arachniodes*) section *Acrorumohra*, which he later (1939) raised to a separate genus. Ching (1964) followed Itô and did not observe the close relationship between the catadromous *D. sparsa* and anadromous *D. macrochlamys*, etc. and placed the two into the two separate genera, *Dryopteris* and *Acrorumohra*. However, Sledge (1973*a* and *b*) commented on the inconsistencies and problems arising from such a treatment and, although at first sight there is a marked difference between the very divided-leaved species such as *D. diffracta* and the less divided ones, Sledge (1973*b*) also pointed out that *D. macrochlamys* (sub *D. obtusissima*) contains a range of form that links the two together, as had been noticed by some earlier authors. The difficulties with this group have also blurred the distinction between *Dryopteris* and *Arachniodes* (and related genera) and though the subgenus *Nephrocystis* is perhaps distantly related to *Arachniodes* and in particular, to *Leptorumohra*, the three genera *Dryopteris, Arachniodes* and *Leptorumohra* appear to be both natural and readily distinguishable. *Nephrocystis* is confined to Africa, Asia, Australasia, and Oceania apart from one species in Central America; most of the species are south-east Asian and Sri Lankan.

Section 1. Purpurascentes Fraser-Jenkins, **sect. nov.**

Frondes magnae, tripinnatae vel quadripinnatae, segmentis parvis remotis asymmetricis. Stipes paleas angustas ferens.

Type: *Dryopteris purpurascens* (Blume) Christ.

Similar to section *Nephrocystis* except that the fronds are large, very well developed, finely dissect, three to four times pinnate and with small, more or less remote ultimate segments which are usually more or less pointed at their apices and auriculate at their acroscopic bases. The rhizome can be either creeping (often markedly so) or, as in section *Nephrocystis*, ascendent. Unlike section *Nephrocystis* the stipe bears very narrow scales particularly in a tuft near the base, and the frond usually bears very small, narrow scales in tufts near the junctions of the rachis, costae, and costules underneath. Some members of this section are perhaps somewhat intermediate in morphology between the rest of subgenus *Nephrocystis* and some members of the section *Marginatae* in subgenus *Dryopteris*, while clearly being closely related to the section *Nephrocystis*. This emphasises the connection between the two subgenera and indicates that *Acrorumohra* is a part of *Dryopteris*.

Contains *c.* 13 species, mainly in south-east Asia and the Australasian and Pacific islands, but extending to Hawaii and Africa and with one species in tropical America. To the section belong *D. futura* A. Reid Smith, *D. kilemensis* (Kuhn) Kuntze, *D. remotipinnulata* Bonap., *D. purpurascens* (Blume) Christ, *D. arborescens* (Baker) Kuntze, *D. wardii* (Baker) Kuntze, *D. permagna* M. Price, *D. dicksonioides* (Mett. ex Kuhn) Copel., *D. powellii* (Baker) C. Chr., *D. pseudoparasitica* Alderw., *D. papuana* C. Chr., *D. parvula* W. Robinson, and *D. pulvinulifera* (Beddome) Kuntze.

Section 2. Nephrocystis

Rumohra section *Acrorumohra* H. Itô in *J. Jap. Bot.* **11**: 583 (August 1935).
Acrorumohra (H. Itô) H. Itô in Nakai & Honda, *Nov. fl. jap.* **4**: 101 (1939 ['1938']).

Type: *Dryopteris hayatae* Tag. (= *D. subexaltata* (Christ) C. Chr.).

Rhizome ascendent; stipe long, bearing ovate-lanceolate scales, rachis and costae more or less glabrous. Fronds medium sized, twice to four times pinnate, becoming a fifth time pinnate in one species, with small, remote segments or large ones, segments normally rounded, asymmetrical.

This section contains less dissected catadromous species showing some similarities to the subgenus *Erythrovariae* as well as to the section *Purpurascentes* and perhaps, though distantly, to the genus *Arachniodes*; it also contains more dissected anadromous species previously placed in the genus *Acrorumohra* (including its type, *D. diffracta*) and showing some similarity to *Leptorumohra*. However the Sri Lankan (Ceylonese) species, *D. macrochlamys*, is remarkable for having both less divided and more divided fronds, even on the same rhizome, thus underlining the connection between the two frond-types.

Contains *c.* 14 species, confined to Asia and the Australasian and Pacific islands and Australia, and well represented in south-east Asia and Sri Lanka: ? *D. aneitensis* (Hook.) C. Chr., *D. hasseltii* (Blume) C. Chr., *D. platypus* (Kunze) Kuntze, *D. sparsa* (Buch.-Ham. ex D. Don) Kuntze, *D. viridescens* (Baker) Kuntze, *D. subexaltata* (Christ) C. Chr., *D. cacaiana* Tag., *D. sabae* (Franchet & P. A. L. Savat.) C. Chr., *D. yoroii* Seriz., *D. deparioides* (T. Moore) Kuntze and subspp., *D. sri-lankensis* Fraser-Jenkins in press, *D. macrochlamys* (Fée) Fraser-Jenkins in press, *D. subreflexipinna* Ogata, and *D. diffracta* (Baker) C. Chr.

Species not placed in the classification

It has not yet been possible to place 12 species, mostly from Hawaii and the south Atlantic islands, into the classification outlined here, as their morphology is not sufficiently close to other species; they need further study to ascertain their natural relationships. The unplaced species are as follows:

Madagascar: *Dryopteris perrieriana* C. Chr., *D. subcrenulata* (Baker) C. Chr.
Hawaii: *Dryopteris acutidens* C. Chr., non Ching, *D. crinalis* (Hook. & Arn.) C. Chr. (probably a *Ctenitis*), *D. glabra* (Brackenr.) Kuntze, *D. nuda* L. Underw., *D. sandwiciensis* (Hook. & Arn.) C. Chr., *D. unidentata* (Hook. & Arn.) C. Chr.
Central America: *Dryopteris nubigena* Maxon & C. Morton.
South Atlantic islands: *Dryopteris ascensionis* (Hook.) Kuntze, *D. cognata* (C. Presl) Kuntze, *D. napoleonis* (Bory) Kuntze. These three species all appear to be related and form a distinct group with a frond shape similar to many *Ctenitis* species; the group needs further study with a view to recognising it taxonomically, perhaps as a fifth subgenus of *Dryopteris* if they belong to *Dryopteris* at all.

New species

1. **Dryopteris subpycnopteroides** Ching ex Fraser-Jenkins, **sp. nov.**

Fig. 1

Species inter *D. conjugatam* et *D. pycnopteroidem* intermedia. Stipes dense paleaceus, lamina aliquanto tenui laevique, pinnis quam eis *D. conjugatae* minus profunde lobatis. Sori in medio pinnae inserti.

Morphology intermediate between that of *D. conjugata* and *D. pycnopteroides*. Stipe densely clothed with narrow, mid-brown scales, which are slightly paler than in *D. conjugata* and more dense than in *D. pycnopteroides*. Lamina slightly larger and wider than in *D. pycnopteroides*, but similar to it in texture and thus thinner, softer, and smoother than in *D. conjugata*, with the veins slightly darkened and presumably very slightly impressed in the upper surface in the living state as in *D. pycnopteroides* and *D. dickinsii*. Pinnae less deeply lobed than in *D. conjugata*, with wide square lobes which are slightly deeper than in normal *D. pycnopteroides*; the lowest pair of pinnae often slightly deflexed and as long as those above, so that the frond has a wide base; pinna-lobes bearing a few long, narrow teeth at the corners. Sori indusiate, medial along the centre of the pinnae reaching close to the costa. Spores of relatively medium size; *c.* 45 μm long. Cytotype unknown.

Holotype: Yunnan, Yangbi, 6 Nov. 1929, *R. C. Ching* 25498 (PE!). Paratypes: Yunnan, Yangbi, *R. C. Ching* 22469 (PE!); Yunnan, Yangbi, 2500m, 4 June 1963, *Jingsajiang* team 4265 (PE!).

The dense scales and more deeply lobed pinnae separate this species quite distinctly from *D. pycnopteroides* to which it is closely related. The somewhat small spores suggest that the species may perhaps be a diploid apomict, but it is to be hoped that living material with more spores may become available from China for further study. *D. subpycnopteroides* is so far known only from Yunnan, SW. China.

2. **Dryopteris parrisiae** Fraser-Jenkins, **sp. nov.**

Fig. 2

Species *D. wallichianae* similis, sed fronde parviora, stipe valde relative longiori, pinnis brevioribus, basibus pinnarum latiore conjunctibus, pinnis apicalibus altiore conjunctibus differt. Cytotypus triploideus.

Morphology similar to *D. wallichiana* but fronds smaller when mature (usually up to *c.* 90 cm long). Stipe relatively much longer (between 2/3 the length to the same length as the lamina) and bearing long, narrow, paler-edged scales with dark streaks near to their centres or bases, sometimes becoming mostly dark. Lamina noticeably more stiffly coriaceous than in *D. wallichiana*, and wide at the base with the lowest pair or pairs of pinnae often somewhat deflexed. Pinnae shorter and pinna-lobes markedly widely fused together up to about half the width of the pinna at their bases (except the first pair on each pinna), much more so than in *D. wallichiana*; lower basiscopic pinnules of the lowest pair of pinnae in larger fronds becoming extended and longer than the acroscopic ones, and curving slightly towards the pinna apex. Pinna-lobe apices markedly truncate, bearing a few wide-based, short teeth. Pinnae at the frond apex joined at their bases over a longer distance than in *D. wallichiana*, thus making the frond apex more caudate. Spores partially abortive. Cytotype triploid (apomictic), $2n = 123$, determined on B. S. Parris' collections of small plants growing at the base of the type plant and cultivated at Chelsea Physic Garden as nos 3396 and 3397 (Gibby, 1985).

Holotype: Papua New Guinea, Western Highlands Province, Tomba Path, Mt Hagen, above Tomba village and saw-mill, on rotting log in very mossy cut-over mid-montane *Nothofagus* forest with much *Pandanus*, locally common, *c.* 2600 m, 19 Sept. 1980, *B. S. Parris & J. P. Croxall* 10295 (K!).

Other specimens seen: Papua, E. side of Lake Myola, Kokoda District, no. 1 sub-district, 2000 m, 22 July 1974, *J. R. Croft* et al., LAE 61928 (L!K!), 61848 (L!), 61615 (L!); Papua, NW. slopes of Mt Giluwe, above Kagoba, 3300 m, 22 Jan. 1979, *J. R. Croft* 728 & *J. I. Marsh* (K!); Papua, E. slopes of Mt. Saruwaged, 4 km

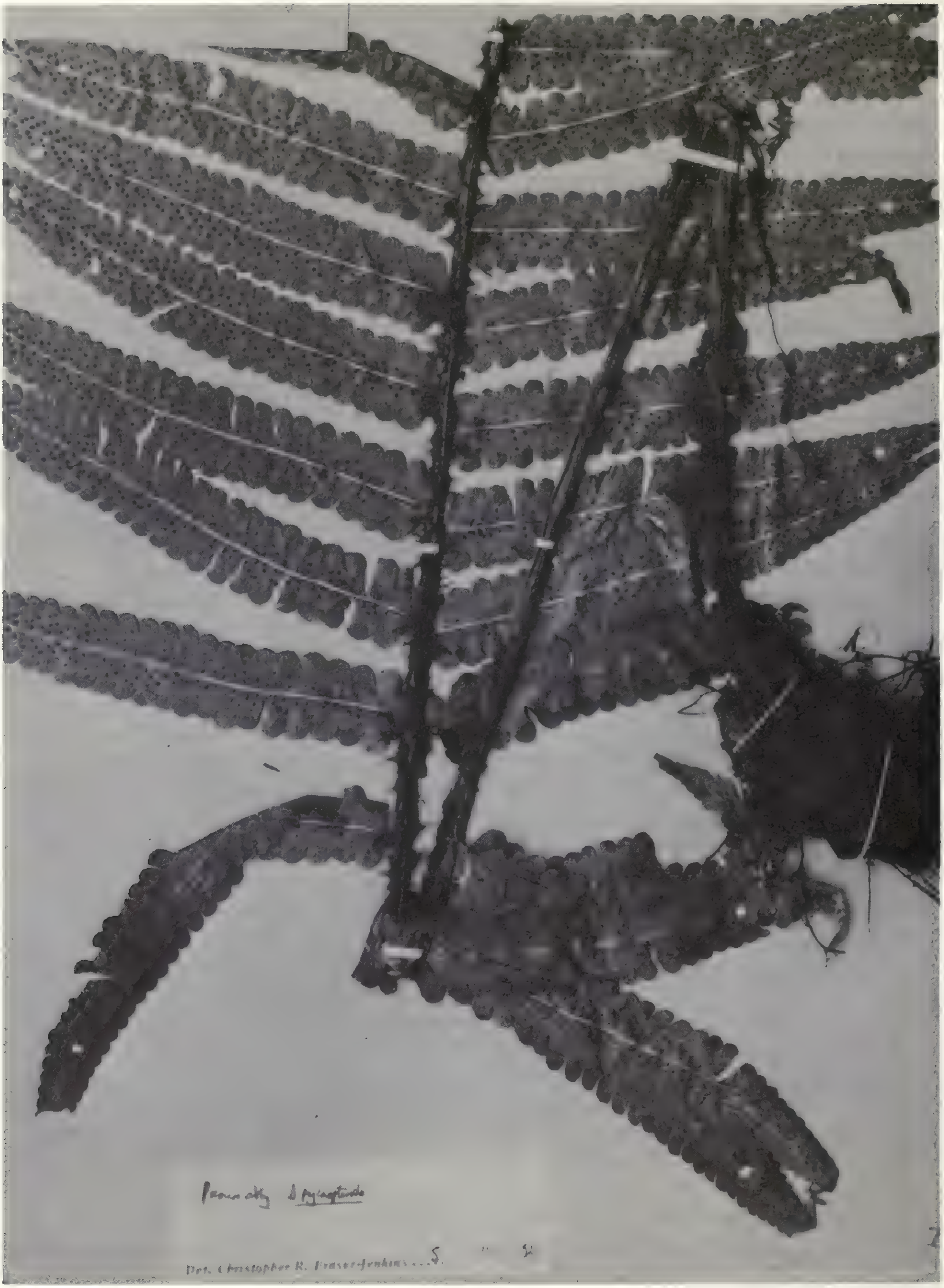
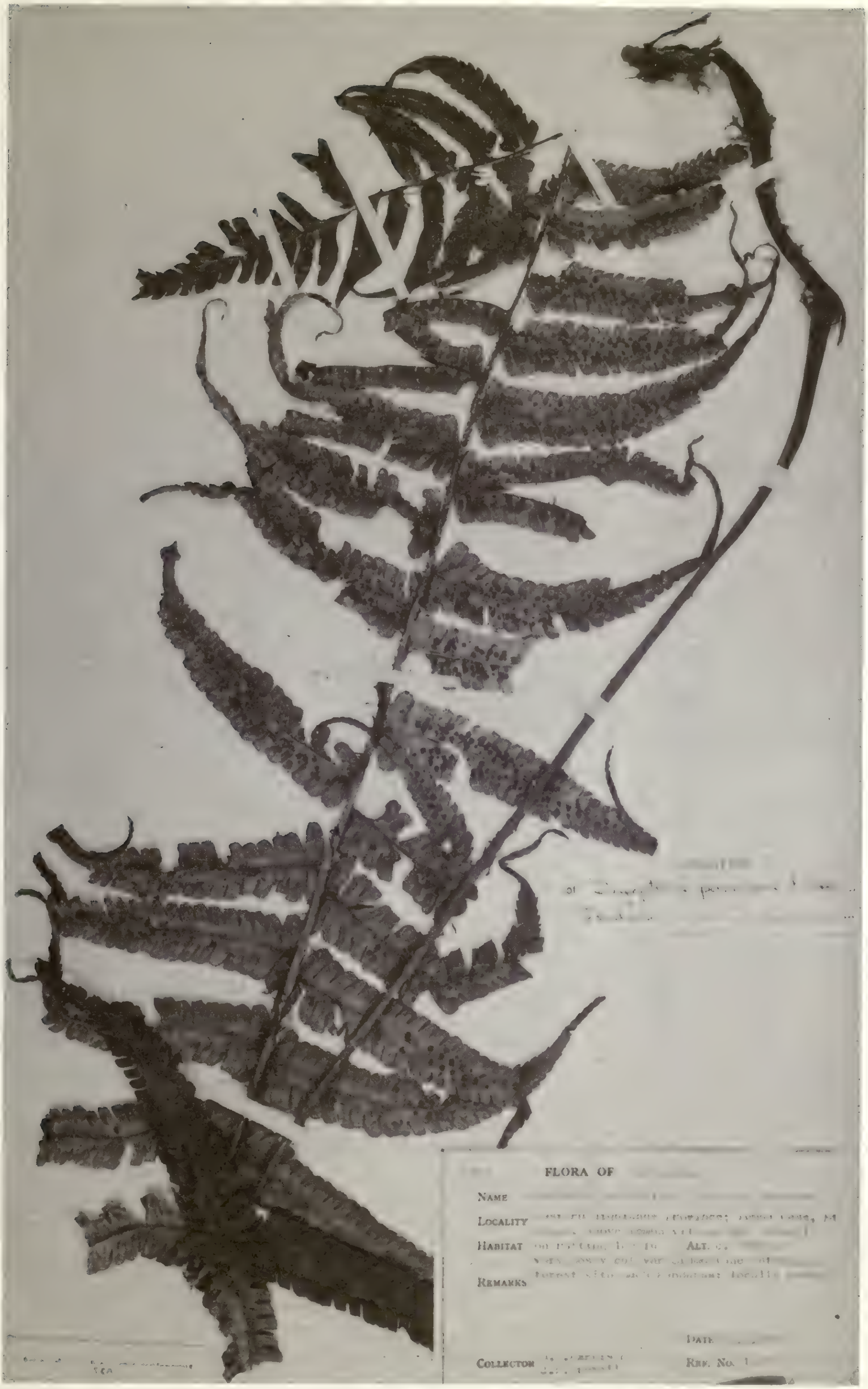

Det. Christopher R. Fraser-Jenkins ... 5.

Fig. 1 *Dryopteris subpycnopteroides* Ching ex Fraser-Jenkins. Holotype (25498) (PE).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REF. NO.

Fig. 2 *Dryopteris parrisiae* Fraser-Jenkins. Holotype (*Parris & Croxall* 10295) (K).

SE. of Lake Gwam, Huon Peninsula, 7 July 1981, *J. R. Croft* 1295 (K!); Papua, Isuani Grassland, SE. slope of Mt Victoria, Port Moresby Subdistrict, Central District, 2700 m, 3 July 1974, *J. R. Croft*, LAE 61615 (K!), 17 July 1974, 61848 (K!); Papua, Mt Giluwe, 3110 m, 18 Aug. 1961, *R Schodde* 1906 (K! L!); New Guinea, Sirunki, Western Highlands, beyond Kaiamanda, 2560 m, young leaves eaten by natives, 4 Sept. 1962, *D. Walker* ANV 651 (K!), 657 (L!); NE. New Guinea, 2440 m, Jan. 1968, *D. Walker* 8836 (K!); Dutch New Guinea, Lake Habbema, 3225 m, *L. J. Brass* 9138 (L! BM!); Papua, Eastern Highlands, Mt Wilhelm, E. slope, 3560 m, 18 June 1959, *L. J. Brass* 30002 (K!L!), 2600 m, 18 July 1959, 30596 (K!L!), 3300 m, 29 June 1959, 30194 (K!L!), 2770 m, 5 July 1959, *L. J. Brass* 30329 (K!); Papua, Milne Bay District, N. slope of Mt Dayman, Maneau Range, 2230–2250 m, 9 June 1953, *L. J. Brass* 22841 (BM!); Papua, Mt Albert Edward, Central Division, 3680 m, May–July 1933, *L. J. Brass* 4409 (BM!); Papua, Ibiwara, *C. Kalkman* 4704 (L!); Papua, South Highlands, Ibiwara, *W. Vink* 17206 (L!), 17220 (L!); Papua, Mt Ambu, *W. Vink* 17399 (L!); Papua, South Highlands, Tari, Mt Né, *W. Vink* 17266 (L!); New Guinea, Kegl Sugl, in forest around camp at ANU store, *c.* 2550 m, 23 Feb. 1970, *A. C. Jermy* 5249 (BM!), 5271 (BM!), 5272 (BM!); New Guinea, Mt Wilhelm, in *Pandanus-Podocarpus* forest, 2700 m, 24 Feb. 1970, *A. C. Jermy* 5257–5260 (BM!); New Guinea, Mount Abilala, in moss forest, *c.* 2740 m, 19 Nov. 1969, *A. C. Jermy* 4265 (BM!); New Guinea, S. side of Lake Naho, Finisterre Mountains, 17 Nov. 1969, *A. C. Jermy* 4220 (BM!).

This species almost replaces *D. wallichiana* in New Guinea, though that species also occurs there as a rarity. Intermediate specimens occur in Java, Borneo, and New Guinea, but are connected to normal *D. wallichiana* by a range of intermediates. Such a plant of *D. wallichiana*, somewhat approaching *D. parrisiae*, but as always more deeply lobed in its pinnae, has been investigated by Gibby (1985) (Sabah, Borneo, Pakka Cave, Kinabalu National Park, 6 Dec. 1980, *A. C. Jermy* 15145 (BM!)) and found to be diploid, $2n = 82$, as in normal *D. wallichiana*. Such plants do not have the extreme *D. parrisiae* morphology, and are presumed to represent variation within *D. wallichiana* as a further example of imitation among closely related *Dryopteris* species, occurring more or less sympatrically. *D. parrisiae* is named after Dr Barbara S. Parris (formerly Croxall) of the Royal Botanic Gardens, Kew, who collected the type specimen. It is so far known only from New Guinea.

3. **Dryopteris tingiensis** Ching & S. K. Wu ex Fraser-Jenkins, **sp. nov.**

Fig. 3

Species *D. barbigerae* subsp. *komarovii* similis, sed paleis stipitis valde fuscioris, lobis pinnarum truncatioribus, sporis maioribus partim abortivis differt.

Morphology similar to *D. barbigera* subsp. *komarovii*, but stipe scales markedly darker and of a castaneous dark brownish black, sometimes with a yellowish tint around their edges. They differ markedly from those of *D. acuto-dentata* by being larger, more numerous, thicker, and without the slightly crinkled, coal-like appearance of the more deciduous scales of that species, as well as in their less black colour, and are thus more similar to those of *D. barbigera* subsp. *komarovii* except in having a markedly darker colour than even the somewhat dark-scaled specimens of the latter that sometimes occur in SE. Tibet and SW. China. Lamina upper surface less glossy and less coriaceous than in *D. acuto-dentata* (which is very slightly coriaceous) and similar to *D. barbigera* subsp. *komarovii*. Pinna-lobes somewhat crowded, incised at the margins in a similar manner to the latter, slightly but recognisably more truncate at their apices, but not as much as in *D. acuto-dentata*. Spores partially abortive, good spores up to *c.* 49 μm long (excluding perispore), and thus larger than in *D. barbigera* subsp. *komarovii*. Cytotype unknown, but the spores suggest that the plant could well be a triploid apomict. It is to be hoped that living material may become available from China for further study.

Holotype: Xizang [Sichang, = Tibet], Kong Chu Hsien, 4200 m, 21 Aug. 1976, *Chang Chung* team 9525 (PE!). Paratype: Xizang [Sichang, = Tibet], Ting Tze Hsien, Ka Ta region, Dang Ga village, 3600–4000 m, 19 June 1976, *Chang Chung* team 4053 (PE!) (spores immature).

This species, though having slightly truncate pinnules, recognisably more so than in *D. barbigera* subsp. *komarovii*, nevertheless looks far closer to it in lamina morphology than to *D. acuto-dentata*, but it is clearly of a different cytotype, from its spores, than the diploid sexual *D. barbigera* subsp. *komarovii*. Ching & Wu named this species, while studying the fern flora of

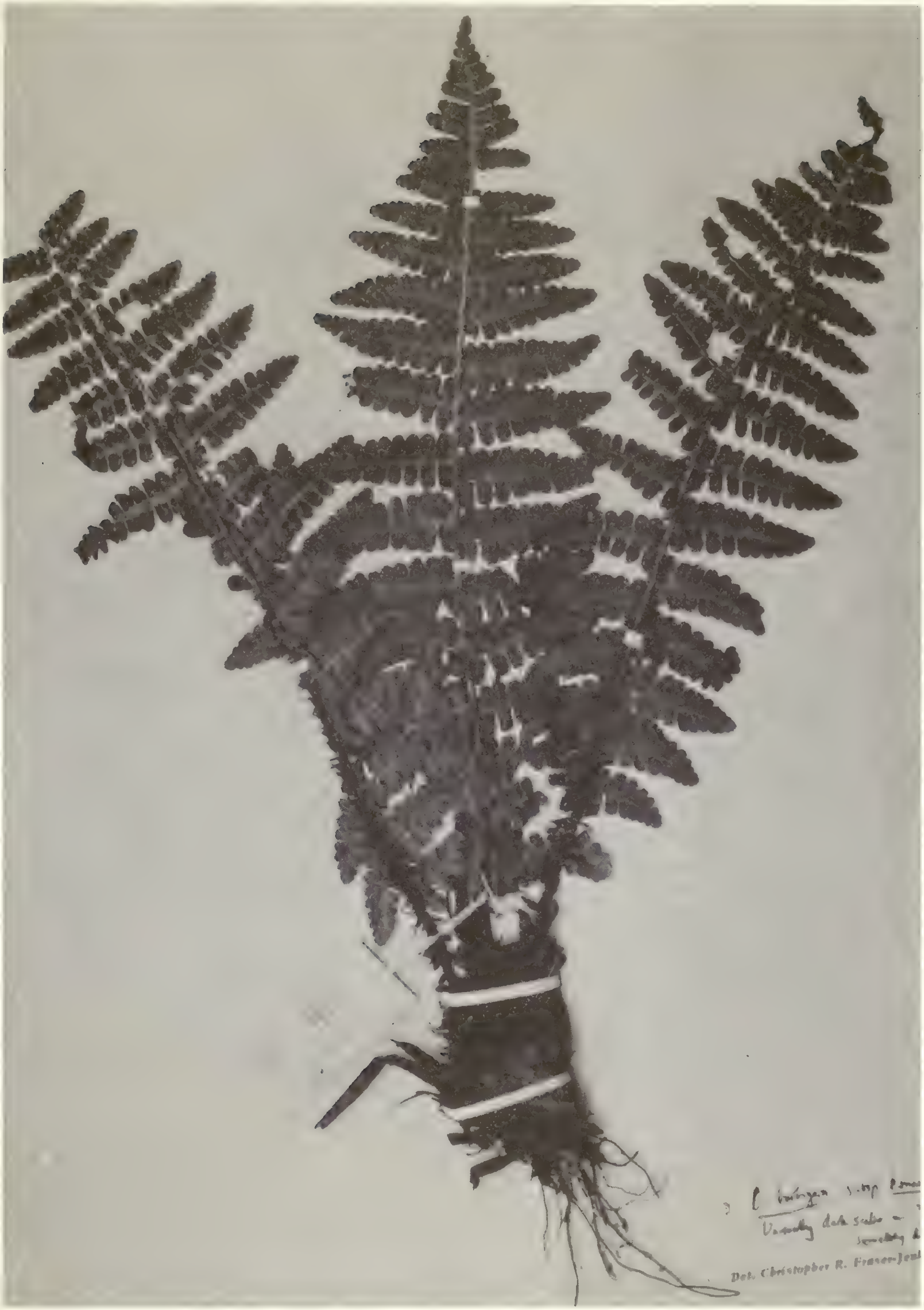
Det. Christopher R. Fraser-Jen

Fig. 3 *Dryopteris tingiensis* Ching & S. K. Wu ex Fraser-Jenkins. Holotype (*Chang Chung* team 9525) (PE).

Tibet, from the single, immature specimen from Ting Tze which has immature spores. Although they have accepted other such specimens for publication as new species, often erroneously, they did not publish *D. tingiensis* along with their other Tibetan species. I agreed with their original recognition of it on seeing the specimen, and became reinforced in my view that it is a new species on studying the specimen that I have designated the type, which was unidentified in a new collection Professor Ching passed to me to examine while I was visiting him in Peking. It is named after Ting Tze county, Tibet, and is so far only known from SE. Tibet.

4. **Dryopteris ruwenzoriensis** C. Chr., **sp. nov.**

Fig. 4

'*Eudryopteris* rhizomate virisimiliter obliquo; stipite valido, 60 cm vel ultra longo, brunneo-stramineo, paleis paucis (plerisque abrasis) luteo-brunneis, lanceolatis, integris, ad 2 cm longis, aliis multo minoribus filiformibus mixtis vestito, superne sulcato. Lamina ovata, magna (metrali?), 60 cm vel ultra lata, papyraceo-herbacea, laete viridi, tripinnata. Pinnis alternis, ad 10 cm inter se remotis, basalibus maximis, ad 35 cm longis, breviter petiolatis, 15 cm latis, latere basiscopico producto inaequilateralibus, acuminatis, sequentibus subaequilateralibus, subdeltoideo-oblongis, subsessilibus, costis sursum alatis; pinnulis II. ord. basiscopicis pinnarum basalium 11–12 cm longis 3 cm latis, pinnis primariis supremis similibus, acroscopicis iis pinnarum ceterum similibus, 4–5 cm longis 1·5–2 cm latis, sessilibus, e basi paulo aequali truncata latiore subgradatim in apicem acuminatum attenuatis omnibus alternis, 3–2 cm inter se remotis, ad costulam plus minusve late alatam profunde pinnatifidis vel majoribus versus basin pinnatis segmentis (vel pinnulis III. ord.) parum obliquis, lateribus parallelis apice truncato rectangularibus, 1–1·5 cm longis 0·5–0·7 mm latis ubique dentatis (dentibus brevibus, deltoideis, non aristatis), majoribus plus minusve profunde serrulato-laciniatis, laciniis subquadratis apice dentatis. Rachi, costis costulisque paleis tenuissimis parvis, lanceolatis, pallide luteo-brunneis sat sparse vestito. Venis in lobis pinnatis, plerisque furcatis, adscendentibus. Soris costularibus, sat magnis, globosis, indusiis non repertis.'

'This new species differs from the many African relatives by its large size, the broad, rectangular ultimate segments with many small teeth and in being (apparently) exindusiate. Small, early falling indusia may possibly be found in quite young sori, but in every case very different from the large indusia of D. Schimperiana (Hochst.) C. Chr., which comes nearest to our species, especially in scale-characters.'

Holotype: Herbarium Filicum Carl Christensen 5112, 22 Juli 1930, Mission H. Humbert-Plantes de l'Afrique Equatoriale – 1929, no. 8825 ter., 'Dryopteris ruwenzoriensis nsp.' [Christensen scripsit]. Massif du Ruwenzori, versant Ouest (Congo Belge, Ituri), Altitude vers 2000 m, Date de la récolte: Juillet (BM!). Paratypes: ditto nos. 8849 (P! BM!); 8900 bis (BM!); Mission Ch. Alluaud Afrique Orientale 1908–1909, no. 303, Ruwenzori (Est), hte. Vall. du Mobuku, montée du Col de Buamba, 3300–3400 m, Janv. 1909 (BM!).

The above diagnosis and comments are typed on a sheet in a capsule mounted with the type specimen at the BM. From the lamina morphology alone it seemed to me that this was a good species, and this was confirmed on examining the spores, which are up to *c.* 42 μm long. These have a remarkable surface of somewhat dense blunt spines, unlike any other *Dryopteris* examined, and do not have clear wings of perispore. In *Dryopteris schimperiana*, which is close to *D. ruwenzoriensis*, the spores are smaller, and have short, more or less clear wings of perispore. The other major difference is the more prominent teeth at the apices of the segments in *D. ruwenzoriensis*, and the often somewhat reddish-brown stipe-base scales; the pinnule-apices are also slightly more obtuse than in many specimens of *D. schimperiana*, and the lamina is laxer. The indusium can be small in *D. schimperiana* on occasions, but is always either small or absent in *D. ruwenzoriensis*. The stipe contains a circle of about six or seven separate vascular strands.

So far *D. ruwenzoriensis* is known only from the Ruwenzori (Mountains of the Moon, Uganda and Zaïre), but it may well occur elsewhere in Africa, and a search in other herbaria may reveal it, identified most probably as *D. schimperiana*.

Other specimens examined: Uganda, Western Province, Toro District, Ruwenzori, Namwamba valley, 3200 m, in heath forest, 6 Jan. 1935, *G. Taylor* 2954 (BM!), on rocks in river, 3170 m, 7 Jan. 1935, *G. Taylor* 2990 (BM!), under *Podocarpus* trees, 2900 m, 11 Jan. 1935, *G. Taylor* 3079a (BM!); Uganda, Western Province, Bigo, River Bujuku, riverside, 3450 m, 23 July 1952, *H. A. Osmaston* 1687 (BM!).

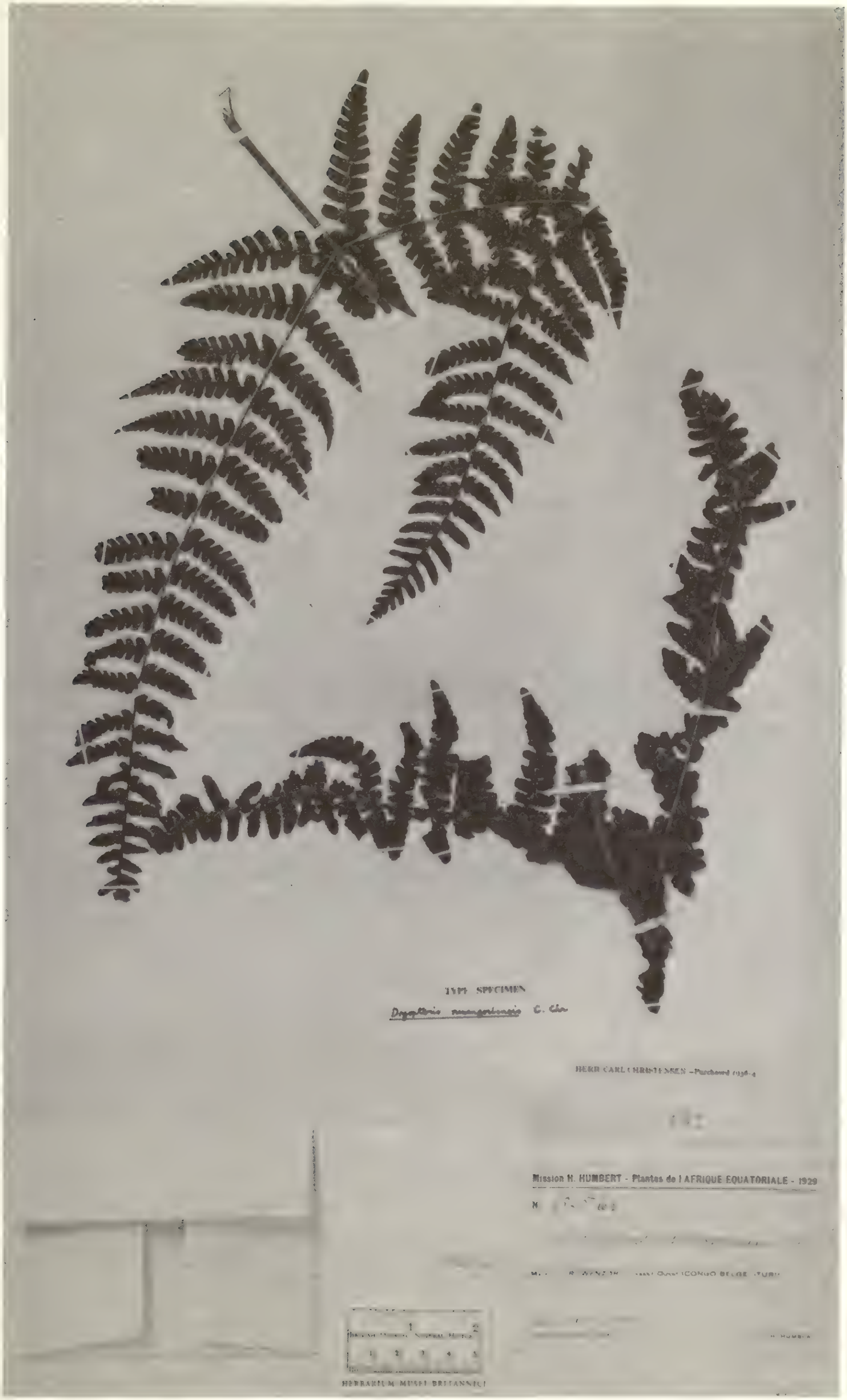
TYPE SPECIMEN
Dryopteris ruwenzoriensis C. Chr.
HERB. CARL CHRISTENSEN – Purchased 1936-4
Mission H. HUMBERT - Plantes de l'AFRIQUE EQUATORIALE - 1929
CONGO BELGE
HERBARIUM MUSEI BRITANNICI

Fig. 4 *Dryopteris ruwenzoriensis* C. Chr. Holotype (*Humbert* 8825) (BM).

Hybrids

A list of 89 naturally occurring *Dryopteris* hybrids (excluding hybrid-derived apomictic or polypoid species), as known to the author, is given below in alphabetical order by regions. However, it should be noted that apart from North America, Europe (in the wide sense) and Japan, search for hybrids has been non-existent or only preliminary; see Fraser-Jenkins (1984: 39–40) for information about the identification of hybrids from spores, etc. The Japanese hybrids are taken from Nakaike (1970, 1975) and Hirabayashi (1974). A useful list of hybrids, though also containing polyploid species, is that of Knobloch (1976), and North American hybrids are taken from this source, and also from Wagner (1970) and Widén, Britton, Wagner & Wagner (1975). Knobloch's list was intended to bring together all the available literature records and did not set out to decide the validity of the hybridity or nomenclature. It has been revised recently by Knobloch, Gibby & Fraser-Jenkins (1984). European hybrids are those verified by the present author after detailed long-term study; thus there are some modifications from published lists and the list here is believed to be definitive for the present. Where the hybrids have not yet been given binomials they are listed after the first parental species, the normal convention of placing the parents in alphabetical order being followed.

Europe (including western Asia, Macaronesia, and north-west Africa) (23):

D. × *ambroseae* Fraser-Jenkins & Jermy (= *D. dilatata* × *D. expansa*); *D.* × *asturiensis* ined. (= *D. affinis* subsp. *affinis* × *D. corleyi*); *D.* × *brathaica* Fraser-Jenkins & Reichst. (= *D. carthusiana* × *D. filix-mas*); *D.* × *cedroensis* Gibby & Widén (= *D. guanchica* × *D. oligodonta*); *D.* × *complexa* Fraser-Jenkins in press, and nothosubspecies (= *D. affinis* subspp. × *D. filix-mas*); *D.* × *deweveri* (J. Jansen) J. Jansen & Wachter (= *D. carthusiana* × *D. dilatata*); *D. expansa* × *D. filix-mas*; *D.* × *euxinensis* Fraser-Jenkins & Corley (= *D. caucasica* × *D. filix-mas*); *D.* × *fraser-jenkinsii* Gibby & Widén (= *D. affinis* subsp. *affinis* × *D. guanchica*); *D.* × *gomerica* Gibby & Widén (= *D. aemula* × *D. guanchica*); *D.* × *graeca* Fraser-Jenkins & Gibby (= *D. pallida* subsp. *pallida* × *D. submontana*); *D.* × *initialis* Fraser-Jenkins & Corley (= *D. caucasica* × *D. oreades*); *D.* × *madalenae* Fraser-Jenkins (= *D. azorica* × *D. crispifolia*); *D.* × *mantoniae* Fraser-Jenkins & Corley (= *D. filix-mas* × *D. oreades*); *D.* × *martinsiae* Fraser-Jenkins (= *D. aemula* × *D. crispifolia*); *D.* × *picoensis* Fraser-Jenkins (= *D. affinis* subsp. *affinis* × *D. azorica*); *D.* × *pseudoabbreviata Jermy* (= *D. aemula* × *D. oreades*); *D.* × *sardoa* Fraser-Jenkins & Reichst. (= *D. oreades* × *D. tyrrhena*); *D.* × *sarvelae* Fraser-Jenkins & Jermy (= *D. carthusiana* × *D. expansa*); *D.* × *sjoegrenii* Fraser-Jenkins (= *D. azorica* × *D. dilatata*); *D.* × *telesii* Fraser-Jenkins (= *D. crispifolia* × *D. dilatata*); *D.* × *uliginosa* (A. Braun ex Doell) Kuntze ex Druce (= *D. carthusiana* × *D. cristata*); *D.* × *vidae* Fraser-Jenkins & Gibby (= *D. pallida* subsp. *pallida* × *D. villarii*).

North America (31):

D. × *algonquinensis* D. Britton (= *D. fragrans* × *D. marginalis*); *D.* × *atropalustris* Small (= *D. celsa* × *D. cristata*); *D.* × *australis* (Wherry) Small (= *D. celsa* × *D. ludoviciana*); *D.* × *benedictii* Wherry (= *D. carthusiana* × *D. clintoniana*); *D.* × *boottii* (Tuckerman) L. Underw. (= *D. cristata* × *D. intermedia*); *D.* × *burgessii* B. Boivin (= *D. clintoniana* × *D. marginalis*); *D. campyloptera* × *D. expansa*; *D. campyloptera* × *D. intermedia*; *D. campyloptera* × *D. marginalis*; ? *D. carthusiana* × *D. celsa*; *D. carthusiana* × *D. goldiana*; *D. celsa* × *D. clintoniana*; *D. celsa* × *D. goldiana*; *D. clintoniana* × *D. cristata*; *D. clintoniana* × *D. goldiana*; ? *D. cristata* × *D. goldiana*; *D.* × *dowellii* (Farw.) Wherry (= *D. clintoniana* × *D. intermedia*); *D. expansa* × *D. intermedia*; *D. expansa* × *D. marginalis*; *D. filix-mas* × *D. goldiana*; *D. filix-mas* × *D. marginalis*; ? *D. fragrans* × *D. intermedia*; *D. goldiana* × *D. intermedia*; *D. intermedia* × *D. marginalis*; *D.* × *leedsii* Wherry (= *D. celsa* × *D. marginalis*); *D.* × *neo-wherryi* W. Wagner (= *D. goldiana* × *D. marginalis*); *D.* × *pittsfordensis* Slosson (= *D. carthusiana* × *D. marginalis*); *D.* × *separabilis* (W. Palmer) Small (= *D. celsa* × *D. intermedia*); *D.* × *slossoniae* Wherry ex Lellinger (= *D. cristata* × *D. marginalis*); *D.* × *triploidea* Wherry (= *D. carthusiana* × *D. intermedia*); *D.* × *uliginosa* (A. Braun ex Doell) Kuntze ex Druce (= *D. carthusiana* × *D. cristata*).

Mainland China and Korea (4):

D. × *daliensis* Z. R. Wang in press (= *D. woodsiisora* × *D. zinongii*); unnamed hybrid of *D. fangii*; ? *D.* × *saxifragi-varia* Nakai (? = *D. bissetiana* × *D. varia*); *D.* × *shuichangensis* Chiu & Yao ex Ching (pro sp.) (= *D. crassirhizoma* subsp. *whangshangensis* × *D. dickinsii*).

Japan (23):

Many of the Japanese hybrids have not been reported clearly enough or with sufficient detail of spores, etc., to ascertain that they are hybrids in the sense of this account; this list could, perhaps, contain some which are apomictic species. *D.* × *fujipedis* Kurata (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. lacera*); *D.* × *gotenbaensis* Nakaike (= *D. hondoensis* × *D. uniformis*); *D.* × *haganecola* Kurata (= *D. cycadina* × *D. uniformis*); *D.* × *hakonecola* Kurata (= *D. dickinsii* × *D. uniformis*); *D.* × *hisatsuana* Kurata (= *D. handeliana* × *D. lacera*); *D.* × *kidoana* Kurata nom. nud. (= ? *D. commixta* × *D.* sp.); *D.* × *kominatoensis* Tag. (= *D. monticola* × *D. tokyoensis*); *D.* × *mayebarae* Tag. (= *D. commixta* × *D. uniformis*); *D.* × *mituii* Seriz. (= *D. lacera* × *D. uniformis*); *D.* × *otomasui* Kurata (= *D. commixta* × ? *D. polylepis* or ? *D. uniformis*); *D.* × *pseudo-commixta* Kurata (= *D. commixta* × *D. dickinsii*); *D.* × *rarissima* Kurata (= *D. commixta* × *D. sparsa*); ? *D.* × *shibisanensis* Kurata (= *D. commixta* × *D. cycadina*); *D.* × *sugino-takaoi* Kurata (= *D. lacera* × *D. polylepis*); *D.* × *tetsu-yamanakae* Kurata (= *D. commixta* × *D. sieboldii*); *D.* × *tokudai* Sugim. (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. polylepis*); *D.* × *toyamae* Tag. (= *D. sieboldii* × ? *D. lacera*); *D.* × *watanabei* Kurata (= *D. crassirhizoma* subsp. *crassirhizoma* × *D. uniformis*); *D.* × *yamashitae* Kurata (= *D. sparsa* × *D. subexaltata*). According to Hirabayashi (pers. comm. 1982) a few other hybrids recently found in Japan are soon to be described, and Nakaike (1982) lists *D.* × *kousaii* Akas., *D.* × *tonensis* Kurata, *D.* × *wakui* Kurata, and *D.* × *yasuhikoana* Kurata.

Indian subcontinent (9):

D. × *flemingii* Fraser-Jenkins in press (= *D. chrysocoma* × *D. juxtaposita*); *D.* × *ghatakii* Fraser-Jenkins in press (= *D. austro-indica* × *D. cochleata*); *D.* × *liddarensis* Fraser-Jenkins in press (= *D. barbigera* subsp. *barbigera* × *D. serrato-dentata*); *D.* × *loyalii* Fraser-Jenkins in press (= *D. caroli-hopei* × *D. marginata*); *D.* × *macdonellii* Fraser-Jenkins in press (= *D. filix-mas* × *D. ramosa*); *D. sparsa* (2×) × *D. sparsa* (4×); *D.* × *vidyae* Fraser-Jenkins in press (= *D. sparsa* × *D. splendens*); *D.* × *wechteriana* Fraser-Jenkins in press (= *D. chrysocoma* × *D. nigropaleacea*); *D.* × *zygo-parentalis* Fraser-Jenkins in press (= *D. darjeelingensis* × *D. scottii*).

List of synonyms

The following is a list of synonyms within the genus *Dryopteris*. The species to which the synonyms are referred may be found listed after each section or in the index. In Christensen's *Index filicum* and supplements (1905–1934), Pichi Sermolli (1965), and Jarrett *et al.* (1985) many more species are placed in Christensen's subgenus *Dryopteris* than in the modern genus *Dryopteris* as he included *Ctenitis* and other closely related genera such as *Nothoperanema*, as well as many thelypteroid ferns, and many that are synonyms of *Dryopteris* species. It is hoped that the present list is nearly complete and will complement the *Index filicum* as far as *Dryopteris* (in the modern sense) is concerned. All the names in *Index filicum* and supplements have been checked and any not appearing in the present list have been excluded from *Dryopteris*.

abbreviata (DC.) Newman ex Manton, non (Schrader) Kuntze = *affinis* subsp. *affinis*
abbreviata auct., non (DC.) Newman ex Manton, nec (Schrader) Kuntze = *oreades*
acutidens Ching in Ching & Wang, non C. Chr. = *purpurella*
adenorachis C. Chr. = *fructuosa*
adiantoides T. Suzuki = *hasseltii*
affinis (Fischer & C. Meyer) Newman ex C. Chr., comb. inval. (in syn.) = *caucasica*
alexeenkoana Fomin = *dilatata*
alpicola Ching & Z. R. Wang, in press = *chrysocoma*
ambigens (Franchet & P. A. L. Savat.) Koidz. = *uniformis*
ambigens '(Nakai) Koidz.' = *uniformis*
ambigua Druce, nom. nud. = × *deweveri*
ambigua Sledge = *deparioides* subsp. *ambigua* (Sledge) Fraser-Jenkins, in press
americana (Fischer ex Kunze) Clute, nom. provis. (inval.) = *campyloptera*
amoena Ching = *kwanzanensis*
amurensis (Milde) Takeda, non Christ = *amurensis*
aneitensis (Hook.) C. Chr. = ? *hasseltii*
angustipinna Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*
aperta (Fée) C. Chr. = *patula*
apicifixa Ching, Boufford & Shing = *fructuosa*
apicisora Ching & Y. T. Hsieh = *peninsulae*

aquilonaris Maxon = *fragrans*
aristata (Villars) Druce, non (G. Forster) Kuntze = *expansa*
assimilis S. Walker = *expansa*
athyrioides (M. Martens & Galeotti) Kuntze = *cinnamomea*
atrata (Kunze) Ching = *hirtipes* subsp. *atrata* (Kunze) Fraser-Jenkins, in press
australis (Ten.) Guadagno = *pallida*
austriaca auct., non (Jacq.) Woynar ex Schinz & Thell. = *dilatata*

balearica (Litard.) Nardi = *pallida* subsp. *balearica* (Litard.) Fraser-Jenkins
barbellata Fomin = *sichotensis*
basiaurita Ching = *dickinsii*
bernieri Tard. = *bojeri*
bipinnata C. Chr. in A. Léveillé, non Copel. = *fuscipes*
blepharolepis C. Chr. = *sublacera*
blinii A. Léveillé = *marginata*
× *bohemica* Domin, nom. inval. = *filix-mas*
× *borbasii* Litard. = *remota*
borreri (Newman) Newman ex Tavel = *affinis* subsp. *borreri* (Newman) Fraser-Jenkins
× *boydii* (Stansf.) C. Morton = *remota*
bullatipaleacea Ching = *championii*
bulligera Ching = *erythrosora*
× *burnatii* Christ & Wilczek = *villarii*
buschiana Fomin = *crassirhizoma* subsp. *crassirhizoma*

callolepis C. Chr. = *antarctica*
canaliculata Ching = *pulcherrima*
canaliculatis Ching ex Fraser-Jenkins, nom. nud. = *pulcherrima*
caudifrons Ching in Ching & Wang = *integriloba*
caudipinna Nakai = ? *erythrosora*
cavalerii A. Léveillé, non (Christ) C. Chr. = *fructuosa*
× *cebennae* Fraser-Jenkins = *tyrrhena*
centro-chinensis Ching = *rosthornii*
changii Ching, non *zhangii* Ching = *championii*
changtouensis Ching ex Fraser-Jenkins, nom. nud. = *pulcherrima*
chapaensis C. Chr. & Ching ex Ching = *polita*
chichisimensis Nakai ex H. Itô = *insularis*
chingii Nair = *pulcherrima*
cochin-chinensis Ching, nom. nud. = *integriloba*
confertipinna Ching & Shing = *fuscipes*
constantissima Hayata = *formosana*
cordipinnula C. Chr. = *remotipinnulata*
coreano-montana Nakai = *sichotensis*
cyrtolepis Hayata = *wallichiana*

decurrentiloba Ching & C. F. Zhang, in press = *uniformis*
dehuaensis Ching & Shing = *bissetiana*
dentipalea Nakai = *uniformis*
discreta Ching & S. K. Wu = *pulcherrima*
dispar Ching & C. F. Zhang, in press = *fuscipes*
× *doeppii* Rothm. = *remota*
doiana Tag. = *wallichiana*
× *doluchanovii* A. Askerov = *remota*
doniana (Spreng.) Ching = *wallichiana*
doshunglaensis Ching & S. K. Wu, nom. nud. = *alpestris*

elongata (Aiton) T. Sim, non (J. Smith) Kuntze = *aitoniana*
elongata '(Sw.) Chev.' = *aitoniana*
emigrans Copel. = *deparioides* subsp. *concinna* C. Chr.
enneaphylla (Baker) C. Chr. = *sieboldii*
espinosai Hicken = *karwinskyana*
euspinulosa (Asch.) Fomin, nom. inval. = *carthusiana*
extremiorientalis V. Vassiljev, nom. nud. = *expansa*

falconeri (Hook.) Kuntze = *barbigera* subsp. *barbigera*
fatuhivensis E. Brown = ? *hirtipes* subsp. *hirtipes*
fenyangshanensis Ching & C. F. Zhang, in press = *cycadina*
fibrillosa (C. B. Clarke) Hand.-Mazz., non (Baker) C. Chr. = *pulcherrima*
fibrillosissima Ching = *pulcherrima*
floridana (Hook.) Kuntze = *ludoviciana*
fournieri (Baker) C. Chr. = *mexicana*
fuliginosa C. Chr. = *cognata*

gamblei (C. Hope) C. Chr. = *stenolepis*
gillespiei Copel. = *aneitensis*
giraldii (Christ) C. Chr. [lectotype: 'Nephrod. non elongatum, sed var. giraldii n. var. Christ, Alla meta del monte Si-Ku-Tzui-San, *J. Giraldi*, [18] Juglio 1894' (P!)] = *sericea*
gongboensis Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press
gracillima Ching = *deparioides* subsp. *gracillima* (Ching) Fraser-Jenkins, in press
grandissima Tag. = *marginata*
grossa (Christ) C. Chr. = *scottii*
gushanica Ching & Shing = *bissetiana*
gushiangensis ['*gushaingensis*'] Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press
gutishanensis Ching & C. F. Zhang, in press = *championii*

harae H. Itô = *pulvinulifera*
hatusimae H. Itô = *hasseltii*
hayatae Tag. = *subexaltata*
heleopteroides Christ = *cochleata*
× *hercynica* Rothm., nom. nud. = *carthusiana*
heterolepia Alderw. = *chaerophyllifolia*
heteroneura (Tag.) Ching = *pseudosieboldii*
hirtosparsa Y. C. Wu, non Christ = *integriloba*
hololepis (Hayata) Tag. = *varia*
hopei Fraser-Jenkins ex Rush, nom. nud. = *caroli-hopei*
huangangshanensis Ching = *rosthornii*
hunanica Ching = *kinkiensis* [juvenile]
hupehensis Ching = *rosthornii*
hwangii Ching = *integriloba*
hypophlebia Hayata = *fructuosa*

immixta Ching = *bissetiana*
indecora (Liebm.) C. Chr. = *cinnamomea*
indusiata (Makino) Makino & Yamamoto ex Yamamoto = *tenuicula*
infrahirtella Ching & Z. Y. Liu, in press = *championii*
infrapuberula Ching, Boufford & Shing = *namegatae*
integripinnula Ching = *cordipinna*
inuyamensis H. Itô = *fuscipes*

jiulungshanensis Chiu & Yao ex Ching = *purpurella*
julaodongensis Ching & Z. R. Wang in Z. R. Wang & Z. X. Zhang, nom. nud. = *rosthornii*
junlianensis Kung = *lepidopoda*

kaihuaensis Ching & C. F. Zhang, in press = *fuscipes*
kemulariae Mikheladze = *remota*
kobayashii Kitagawa = *sacrosancta*
kodamae Hayata = *formosana*
komarovii Kossinsky = *barbigera* subsp. *komarovii* (Kossinsky) Fraser-Jenkins, in press
kongboensis Ching ex Fraser-Jenkins, nom. nud. = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press
kooshiangensis Ching ex Fraser-Jenkins, nom. nud. = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press
koraiensis Tag. = *gymnophylla*
kuratae Nakaike, nom. nud. = ? *hangchowensis*

labordei (Christ) C. Chr. = *gymnosora*
laeta (V. Komarov) C. Chr., non (Sw.) C. Chr. = *goeringiana*

lanceolato-cristata (Hoffm.) Alston = *carthusiana*
lancifrons Hayata ex Fraser-Jenkins, nom. nud. = *fructuosa*
lancipinnula Ching, nom. nud. = *subimpressa*
× *laschii* E. Walter = × *uliginosa*
laserpitiifolia (Scortech. ex Beddome) C. Chr., non (Mett.) Kuntze = *hasseltii*
lastii (Baker) C. Chr. = *kilemensis*
latibasis Ching = *lepidopoda*
laurisilvicola T. Suzuki = *polita*
× *lawalreei* Janchen = *remota*
layardii (Baker) C. Chr. = *aneitensis*
lepidorachis C. Chr. = *championii*
lepinei (Kuhn) Kuntze = *dicksonioides*
leveillei Nakai, non Christ = *marginata*
libanotica (Rosenstock) C. Chr. = *pallida* subsp. *libanotica* (Rosenstock) Nardi
likiangensis Ching, non *lichiangensis* (C. H. Wright) C. Chr. = *montigena*
liliana Golicin [Golitsin] = *aemula*
linganensis Ching & C. F. Zhang, in press = *championii*
lingtzeensis Ching ex Fraser-Jenkins, nom. nud. = *sublacera*
linyingensis Ching & C. F. Zhang, in press = *erythrosora*
× *litardierei* Rothm. = *oreades*
lividis Ching & C. H. Wang = *polita*
liyangensis Ching & Lan = ? *erythrosora*
longistipes Ching = *lepidopoda*
ludens (Baker) C. Chr. = *arborescens*

macaronesica Romariz = *aitoniana*
macrocarpa R. Stewart = *chrysocoma*
× *madeniana* Kunkel, nom. nud. = *oligodonta*
maderensis Milde ex Alston = *intermedia* subsp. *maderensis* (Milde ex Alston) Fraser-Jenkins
makinoi Koidz. = *fuscipes*
manshurica Ching ex Wang et al. = *expansa*
matsuzoana Koidz. = *varia*
maxima (Baker) C. Chr. = *arborescens*
medioxima Koidz. = *fuscipes*
mediterranea Fomin = *wallichiana*
mehrae Khullar, nom. nud. = *blanfordii* subsp. *blanfordii*
melanocarpa Hayata = *platypus*
melanolepis (Alderw.) Alderw., comb. inval. (in syn.) = *scottii*
metafuscipes Ching & C. F. Zhang, in press = *erythrosora*
metcalfii Ching = *marginata*
mimetica Ching & C. F. Zhang, in press = *cordipinna*
mingetsensis Hayata ex Fraser-Jenkins, nom. nud., non *mingetsuensis* Hayata = *fructuosa*
mingetsuensis Hayata = *reflexosquamata*
minimisora Nakai = *expansa*
minjiangensis Kung = *sublacera*
× *mixta* Rothm., nom. nud., non Rosenstock = × *mantoniae*
monticola (Makino) C. Chr. = *goldiana* subsp. *monticola* (Makino) Fraser-Jenkins
morrisonensis (Hayata) Hayata = *expansa*
multijugata Ching & Shing ex Ching & C. F. Zhang, in press = *fuscipes*

nakanensis Ching = *microlepis*
nanchuanensis Ching & Liu, in press = *tenuicula*
× *neglecta* Domin, non Brade & Rosenstock = ? × *deweveri*
neoassamensis Ching = *assamensis*
neochrysocoma Ching = *woodsiisora*
neolacera Ching = *peninsulae*
neolepidopoda Ching & S. K. Wu = *lepidopoda*
neopodophylla Ching = *podophylla*
nigra Ching = *lepidopoda*
nigrisquama Hayata = *scottii*

nigrosquamosa Ching = *blanfordii* subsp. *nigrosquamosa* (Ching) Fraser-Jenkins, in press
nilamoensis Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*
nipponensis Koidz. = *cystolepidota*
nyalamensis [‘*nyalamense*’] Ching & S. K. Wu = *pulcherrima*
nyingchiensis Ching = *sublacera*

obovata (Baker) C. Chr. = *hasseltii*
obtusissima (Makino) Makino, non (Mett. ex Kuhn) Christ = *fuscipes*
obtusissima (Mett. ex Kuhn) Christ, non (Makino) Makino = *macrochlamys*
odontophora Copel. = *aneitensis*
ogawae [‘*ogawai*’] H. Itô = *varia*
okushirensis Miyabe & Kudô = *dickinsii*
omeicola Ching = *rosthornii*
oxyodon (Franchet) Kitagawa, non *oxyodus* (Baker) C. Chr. = *goeringiana*

pachyphylla Hayata = *wallichiana*
paleacea Hand.-Mazz., non (Lagasca ex Sw.) C. Chr., nec (T. Moore) Fomin = *wallichiana*
paleacea (Lagasca ex Sw.) C. Chr., non Hand.-Mazz., nec (T. Moore) Fomin = *wallichiana*
paleacea (T. Moore) Fomin, non (Lagasca ex Sw.) C. Chr., nec Hand.-Mazz. = *wallichiana*
paleacea ‘(Don) Druce’ = *wallichiana*
paleacea ‘(Don) Hand.-Mazz.’ = *wallichiana*
paleacea ‘(Sw.) Hand.-Mazz.’, comb. inval. = *wallichiana*
pallida ‘(Bory) Fomin’ = *pallida*
pandurata Ching ex Fraser-Jenkins, nom. nud. = *basisora*
para-chrysocoma Ching & Z. R. Wang = ? *chrysocoma*
parallelogramma (Kunze) Alston = *wallichiana*
parasparsa Ching & S. K. Wu = *sparsa*
patagonica Diem = *filix-mas*
patentissima (Wallich ex Kunze) Nair = *wallichiana*
patentissima ‘(Franch.) Nair’ = *wallichiana*
persimilis Ching & C. F. Zhang, in press = *fuscipes*
petelotii C. Chr. = *polita*
phaeocoma Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *lepidopoda*
phaeolepis Hayata = *formosana*
platylepis Rosenstock = *kilemensis*
poilanei Tard. = *bodinieri*
× *poyseri* Wherry = *clintoniana*
pseudatrata Ching = *cycadina*
pseudoerythrosora Ching & C. F. Zhang, in press, non Kodama = *erythrosora*
pseudo-erythrosora Kodama, non Ching & C. F. Zhang = *championii*
pseudodontoloma Ching = *lachoongensis*
pseudofibrillosa Ching = *redactopinnata*
pseudo-filix-mas Nakai & Kodama, nom. nud., non (Fée) Rothm. = *crassirhizoma* subsp. *crassirhizoma*
pseudo-lunanensis Tag. = *dickinsii*
pseudomarginata Ching, nom. nud. = *caroli-hopei*
pseudomas (Wollaston) Holub & Pouzar = *affinis* subsp. *affinis*
pseudo-sabae [‘*pseudo-sabaei*’] Hayata = *fructuosa*
pseudo-sikkimensis Ching & S. K. Wu = *sikkimensis*
pseudosparsa Ching = *purpurella*
pseudouniformis Ching = *uniformis*
pseudovaria (Christ) C. Chr. = *fructuosa*
psilosora Tag. = *hasseltii*
pudouensis Ching, in press = *pacifica*

qamdoensis Ching = *pulcherrima*
quatanensis Ching = *wallichiana*

raddeana (Fomin) Fomin = *pallida* subsp. *raddeana* (Fomin) Nardi
raynalii Tard. = *manniana*
reflexipinna Hayata = *diffracta*
reholttumii M. Price, nom. nud. = *pulvinulifera*

remota '(A. Br.) Hayek' = *remota* (A. Braun ex Doell) Druce, non Hayata
remotipinnata Ching & C. F. Zhang, in press = *fuscipes*
remotissima (Christ ex Matsum.) Koidz. = *sabae*
resendeana Rezende-Pinto = *affinis* subsp. *affinis*
retroso-paleacea Ching & C. F. Zhang, in press = *cordipinna*
rhomboideo-ovata H. Itô = *hondoensis*
rigida (Sw.) A. Gray = *villarii*
rigida '(Hoffm. ex Sw.) Gray' = *villarii*
rigida '(Sw.) Underw.' = *villarii*
rossii (C. Chr.) C. Chr. = ? *glandulifera*
rubristipes Ching & Z. Y. Liu, in press = *purpurella*

saamingensis Ching = *tokyoensis*
sakuraii (Rosenstock) Tag. = *gymnophylla*
× *satsumana* Kurata = × *pseudo-commixta*
schneideriana Hand.-Mazz. = *sublacera*
× *schorapanensis* A. Askerov = *affinis* subsp. *persica* Fraser-Jenkins
semipinnata Ching = *lunanensis*
setosa (Christ) Kudô, non (Thunb.) Akas., nec (Blume) Kuntze, nec (C. Presl) C. Chr. = *sichotensis*
setosa (Thunb.) Akas., non (Blume) Kuntze, nec (C. Presl) C. Chr., nec (Christ) Kudô = *bissetiana*
shensicola Ching & Y. T. Hsieh = *peninsulae*
silaensis Ching = *acuto-dentata*
simulans Ching, non (Baker) Kuntze = *sri-lankensis*
sinoerythrosora Ching & Shing = *erythrosora*
sinofibrillosa Ching = *pulcherrima*
sinosparsa Ching & Shing = *viridescens*
siranensis Nakai = *expansa*
spinulosa (Roth) Kuntze = *carthusiana*
spinulosa '(Müll. ex Roth) O. Ktze.' = *carthusiana*
squamifera [*'squamigera'*] Ching & S. K. Wu = *pulcherrima*
× *subalpina* (Borbás) Domin, non Alderw. = *remota*
subassamensis Ching = *subtriangularis*
subatrata Tag. = *cycadina*
× *subaustriaca* Rothm. = *remota*
subbarbigera Ching = *barbigera* subsp. *komarovii* (Kossinsky) Fraser-Jenkins, in press
subdecipiens Hayata = *scottii*
subintegriloba Seriz. = *integriloba*
sublaeta Ching & Y. P. Hsu = *goeringiana*
submarginalis Ching, Boufford & Shing = *crassirhizoma* subsp. *whangshangensis* (Ching) Fraser-Jenkins
submarginata Loyal, non Rosenstock = *subimpressa*
submarginata Rosenstock, non Loyal = *tenuicula*
submonticola Nakai = *goldiana* subsp. *monticola* (Makino) Fraser-Jenkins
subodontoloma Ching ex Loyal, nom. nud. = *subimpressa*
subopposita Kodama ex Nakai, non Kuntze ex T. Mori = *expansa*
subramosa Christ = *goeringiana*
sunnii Ching = *pycnopteroides*
supraimpressa Ching, Boufford & Shing = *porosa*

tabacicoma Alderw. = *subarborea*
tahmingensis Ching = *integriloba*
taitoensis Tag., non *taitunensis* Koidz. = *polita*
taiwanicola Tag. = *lepidopoda*
takesimensis Kodama ex Nakai = *erythrosora*
takeuchiana Koidz. = *formosana*
taquetii Christ = *erythrosora*
tarningensis Ching = *fuscipes*
tasiroi Tag. = *handeliana*
× *tauschii* (Čelak.) Domin = × *uliginosa*
× *tavelii* Rothm. = *affinis* subsp. *borreri*
tenuissima Tag. = *woodsiisora*

thibetica (Franchet) C. Chr. = *dickinsii*
thwaitesii (Baker) Kuntze, non (Hook.) C. Chr. = *deparioides* subsp. *concinna* C. Chr.
tieluensis Ching & Y. P. Hsu = *basisora*
tienmohshangensis Ching = *uniformis*
triangularifrons Ching = *gymnosora*
tsangpoensis Ching = *redactopinnata*
tsayüensis Ching & S. K. Wu ex Fraser-Jenkins, nom. nud. = *pulcherrima*
tsutsuiana Kurata = *namegatae*

undulata (Beddome) Kuntze = *macrochlamys*
uropinna M. Price = *subtriangularis*
ursipes Hayata = *wallichiana*

venosa Ching & S. K. Wu = *lachoongensis*
vescoi (Drake) C. Chr. = *dicksonioides*
villarsii auct. = *villarii*
viridis Ching = *polita*

wenchuanensis Kung = ? *habaensis*
whangshangensis Ching = *crassirhizoma* subsp. *whangshangensis* (Ching) Fraser-Jenkins
wherryi Crane = *celsa*
wladiwostokensis B. Fedtsch. = *goeringiana*
× *woynarii* Rothm. = *remota*
wuyishanensis Ching = *kinkiensis*

xanthomelas (Christ) C. Chr. = *rosthornii*

yabei Hayata = *varia*
yakusilvicola Kurata = *cacaiana*
yandongensis Ching & C. F. Zhang, in press = *kinkiensis*
yaoi Ching = *tenuicula*
yikungensis Ching ex Fraser-Jenkins, nom. nud. = *yigongensis*
yui Ching = *bonatiana*
yungtzeensis Ching = *dickinsii*
× *yuyamae* Kurata = × *hakonecola*

zayüensis Ching & S. K. Wu = *pulcherrima*
zhangii Ching, in press, non *changii* Ching = *tenuicula*

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Taxonomic index

Accepted names are given in roman and synonyms in *italic*; new names and principal page references are in **bold**. An asterisk (*) denotes a figure. See pp 207–213 for a list of synonyms.

Acrorumohra 186, 187, 188, 197, 198
Arachniodes 185, 186, 188, 195, 197, 198
Arthrobotrys 187
  macrocarpa 187
Aspidiaceae 184, 185
Aspidiineae 184
Aspidium 184, 188
  Dichasium, subgen. 190
  Diclisodon, group 197
  Filix-mas, group 191
  Fragrantia, group 191
  patentissimum 188
  Sparsa, group 197
  Spinulosa, group 195
Aspleniaceae 184
Athyriaceae 184

Byrsopteris 188

Ctenitis 185, 186, 195, 198, 207
  apiciflora 185

Dennstaedtiaceae subfam. Dryopteridoideae 184
Dichasium 188, 190
Diclisodon 188
  deparioides 188
Dryopsis 185
Dryopteridaceae 184, 185
Dryopteris *abbreviata* 192
  acutidens 198
  acuto-dentata 191, 202, 212
  aemula 194, 195, 210
  Aemulae, sect. 183, 187, **194**, 195
  affinis 191
  affinis subsp. affinis 207, 211, 212
  affinis subsp. borreri 208, 212
  affinis subsp. persica 212
  aitoniana 193, 208, 210
  × algonquinensis 206
  alpestris 192, 208
  × ambroseae 206
  amurensis 195, 207
aneitensis 198, 209, 210, 211
angustifrons 194
antarctica 195, 208
approximata 194
aquilinoides 194
arborescens 198, 210
ardechensis 192
arguta 193
ascensionis 198
assamensis 195, 196, 210
× asturiensis 206
athamantica 194
× atropalustris 206
× australis 206
austro-indica 191
azorica 195
bamleriana 193
barbigera 192
barbigera subsp. barbigera 209
barbigera subsp. komarovii 202, 209, 212
basisora 193, 211, 213
× benedictii 206
bissetiana 197, 208, 209, 212
blanfordii 192
blanfordii subsp. blanfordii 210
blanfordii subsp. nigrosquamosa 209, 211
bodinieri 189, 211
bojeri 194, 208
bonatiana 191, 213
× boottii 206
× brathaica 206
Bulligerae, sect. 187, 196
burgessii 206
cacaiana 198, 213
campyloptera 195, 207
campyloptera × expansa 206
campyloptera × intermedia 206
campyloptera × marginalis 206
caroli-hopei 194, 209, 211
carthusiana 195, 208, 209, 210, 212
carthusiana × celsa 206
carthusiana × goldiana 206
caucasica 192, 207
caudipinna 196
× cedroensis 206
celsa 191, 213
celsa × clintoniana 206
celsa × goldiana 206
chaerophyllifolia 194, 209
championii 196, 208, 209, 210, 211
chinensis 195
chrysocarpa 191
chrysocoma 191, 207, 210, 211
cinnamomea 193, 194, 208, 209
Cinnamomeae, sect. 183, 187, 188, 190, **193**
clintoniana 191, 211
clintoniana × cristata 206
clintoniana × goldiana 206
cochleata 187, 194, 209
cognata 198, 209
commixta 190
× complexa 206
conjugata 190, 199
cordipinna 196, 209, 210, 212
coreano-montana 192
corleyi 192
costalisora 191
crassirhizoma 191
crassirhizoma subsp. crassirhizoma 208, 211
crassirhizoma subsp. **whangshangensis** 183, 191, 212, 213
crinalis 198
crispifolia 195
cristata 191
cristata × goldiana 206
cycadina 190, 209, 211, 212
Cycadinae, subsect. 190
cyclopeltidiformis 195, 196
cystolepidota 196, 211
× daliensis 206
darjeelingensis 190
decipiens 196
deparioides 188, 198

Dryopteris contd.
  deparioides subsp. ambigua 207
  deparioides subsp. concinna 208, 213
  deparioides subsp. gracillima 209
  × deweveri 206, 207, 210
  Dichasium, subsect. 190
  dickinsii 190, 199, 208, 211, 213
  dicksonioides 198, 210, 213
  Diclisodon, group 197
  diffracta 197, 198, 211
  dilatata 187, 195, 207, 208
  × dowellii 206
  dracomontana 194
  Dryopteris, subgen. 186, 187, **189**, 193, 195, 197, 198, 207
  Dryopteris, sect. 187, 190, **191**, 192, 193, 194
  erythrosora 195, 196, 208, 210, 211, 212
  Erythrovariae, sect. 186, 187, **196**
  Erythrovariae, subgen. 183, 186, 187, 188, 190, **195**, 196, 197, 198
  Erythro-variae, subsect. 196
  esterhuyseniae 194
  Eudryopteris, sect. 189, 190, 192
  Eudryopteris, subgen. 189
  × euxinensis 206
  expansa 195, 208, 210, 212
  expansa × filix-mas 206
  expansa × intermedia 206
  expansa × marginalis 206
  fadenii 194
  fangii 191
  fatuhivensis 190
  fibrillosa 190
  Fibrillosae, sect. 186, 187, 188, **190**, 191, 192
  filix-mas 188, 189, 190, 191, 192, 208, 211
  filix-mas × goldiana 206
  Filix mas, group 192
  filix-mas × marginalis 206
  × flemingii 207
  formosana 197, 208, 209, 211, 212
  Formosanae, subsect. 196
  fragrans 192, 208
  fragrans × intermedia 206
  Fragrantes, subsect. 192
  × fraser-jenkinsii 206
  fructuosa, 193, 207, 208, 209, 210, 211
  × fujipedis 207
  fuscipes 196, 208, 209, 210, 211, 212
  fusco-atra 191
  futura 198
  × ghatakii 207
  glabra 198
  glandulifera 194, 212
  goeringiana 194, 209, 211, 212, 213
  goldiana 192
  goldiana subsp. **monticola** 184, 192, 210, 212
  goldiana × intermedia 206
  × gomerica 206
  × gotenbaensis 207
  × graeca 206
  guanchica 195
  gymnophylla 195, 209, 212
  gymnosora 196, 209, 213
  Gymnosorae, subsect. 196
  habaensis 191, 213
  hadanoi 197
  × haganecola 207
  × hakonecola 207, 213
  handeliana 190, 212
  hangchowensis 190, 209
  hasseltii 198, 207, 209, 210, 211
  hawaiiensis 191
  hayatae 197, 198
  himachalensis 191
  Hirtipedes, sect. 183, 187, 188, **190**, 191
  hirtipes 190
  hirtipes subsp. atrata 208
  hirtipes subsp. hirtipes 209
  × hisatsuana 207
  hondoensis 196, 212
  huberi 194
  inaequalis 188, 194
  incisolobata 191
  × initialis 206
  insularis 197, 208
  integriloba 195, 196, 208, 209, 212
  intermedia 195
  intermedia subsp. maderensis 210
  intermedia × marginalis 206
  juxtaposita 193
  karwinskyana 194, 208
  kenzoi 196
  khullarii 191
  × kidoana 207
  kilemensis 198, 210, 211
  kinkiensis 196, 209, 213
  kinokuniensis 196
  koidzumiana 196
  × kominatoensis 207
  × kousaii 207
  kwanzanensis 193, 207
  lacera 193
  lachoongensis 193, 211, 213
  laurisilvicola 196
  × leedsii 206
  lepidopoda 191, 209, 210, 211, 212
  lewalleana 194
  liankwangensis 190
  × liddarensis 207
  liyangensis 196
  Lophodium, group 195
  Lophodium, sect. 187, 192, 194, **195**
  × loyalii 207
  ludoviciana 191, 209
  lunanensis 190, 212
  × macdonnellii 207
  macrochlamys 197, 198, 211, 213
  × madalenae 206
  madrasensis 191
  mangindranensis 194
  manniana 194, 211
  × mantoniae 206, 210
  marginalis 187, 193
  marginata 194, 208, 209, 210
  Marginatae, sect. 183, 187, 190, 192, **194**, 195, 198
  × martinsiae 206
  maxonii 194
  × mayebarae 207
  meeteetseana 184
  mexicana 194, 209
  microlepis 190, 210
  mindshelkensis 192
  × mituii 207
  Monticolarum, subsect. 192
  montigena 192, 210
  munchii 194
  namegatae 190, 209, 213
  napoleonis 198
  neorosthornii 191
  × neo-wherryi 206
  Nephrocystis, sect. 186, 187, 197, **198**
  Nephrocystis, subgen. 183, 185, 186, 187, 193, 196, **197**, 198
  nigropaleacea 193
  nobilis 191
  nubigena 198
  nuda 198
  obtusissima 197
  odontoloma 193
  oligodonta 194, 210
  oreades 192, 207, 210
  × otomasui 207
  pacifica 197, 211
  paleacea var. *madagascariensis* 184, 191
  pallida 192, 193, 208, 211
  pallida subsp. balearica 208
  pallida subsp. libanotica 210
  pallida subsp. raddeana 211
  Pallidae, sect. 183, 187, 190, **192**, 193, 194
  panda 191
  Pandae, sect. 183, 187, **191**, 193
  papuana 198
  parachrysocoma 191
  parrisiae 184, 191, **199**, 201*
  parvula 198
  patula 194, 207
  peninsulae 193, 207, 210, 212
  pentheri 194
  permagna 198
  perrieriana 198
  × picoensis 206
  × pittsfordensis 206
  platypus 198, 210
  podophylla 189, 210
  polita 195, 196, 208, 210, 211, 212, 213
  Politae, sect. 183, 187, **196**
  polylepis 191
  Polysticho-drys, sect. 186, 195, 196
  porosa 194, 212
  powellii 198
  × pseudoabbreviata 206

Dryopteris contd.
× pseudo-commixta 207, 212
pseudo-filix-mas 191
pseudoparasitica 198
pseudosieboldii 189, 209
pteridiiformis 194
pulcherrima 190, 191, 207, 208, 209, 211, 212, 213
pulvinulifera 198, 209, 211
purpurascens 197, 198
Purpurascentes, sect. 183, 187, **197**, 198
purpurella 196, 207, 209, 211, 212
Pycnopteris, group 189
Pycnopteris, subgen. 186, 187, **189**, 190
Pycnopteris, subsect. 189
pycnopteroides 190, 199, 212
ramosa 194
× rarissima 207
redactopinnata 191, 211, 213
reflexosquamata 193, 210
reichsteinii 184, 191
remota 192, 208, 209, 210, 212, 213
Remotae, sect. 183, 186, 187, 191, **192**
remotipinnulata 198, 208
rosthornii 191, 208, 209, 211, 213
rubripes 193
ruwenzoriensis 184, 194, **204**, 205*
ryo-itoana 196
sabae 198, 212
sacrosancta 197, 209
saffordii 194
sandwiciensis 198
× sardoa 206
× sarvelae 206
saxifraga 197
× saxifragi-varia 206
schimperiana 194, 204
schnellii 194
scottii 190, 209, 210, 212
× separabilis 206
sericea 193, 209
serrato-dentata 192
shibipedis 197
× shibisanensis 207
shiroumensis 194
× shuichangensis 206
sichotensis 192, 208, 212
sieboldii 188, 189, 208
sikkimensis 193, 211
simasakii 196
× sjoegrenii 206
sledgei 191
× slossoniae 206
sordidipes 197
sparsa 188, 197, 198, 211
sparsa × sparsa 207
spinulosa 195, 212
splendens 193
Splendentes, sect. 183, 187, 190, **193**
sri-lankensis 198, 212
stenolepis 190, 209
stewartii 193
subarborea 194, 212
subcrenulata 198
subexaltata 197, 198, 209
subimpressa 194, 210, 212
sublacera 193, 208, 210, 211, 212
submontana 193
subpycnopteroides 184, 190, **199**, 200*
subreflexipinna 198
subtriangularis 196, 212, 213
× sugino-takaoi 207
× telesii 206
tenuicula 196, 209, 210, 212, 213
tenuipes 196
× tetsu-yamanakae 207
tingiensis 184, 192, **202**, 203*
× tokudai 207
tokyoensis 191, 212
× toyamae 207
× tonensis 207
× triploidea 206
tsugiwoi 196
tyrrhena 192, 208
× uliginosa 206, 210, 212
unidentata 198
uniformis 193, 207, 208, 211, 213
varia 196, 197, 209, 210, 211, 213
Variae, sect. 183, 186, 187, **196**
× vidae 206
× vidyae 207
villarii 192, 208, 212, 213
viridescens 198, 212
× wakui 207
wallichiana 188, 191, 199, 202, 208, 210, 211, 213
wardii 198
× watanabei 207
× wechteriana 207
whangshangensis 191
woodsiisora 191, 210, 212
× yamashitae 207
× yasuhikoana 207
yenpingensis 195, 196
yigongensis 191, 213
yoroii 198
zinongii 191
× zygo-parentalis 207

Elaphoglossaceae 184

Hypodematiaceae 184

Lastrea 184, 188
Arthrobotrys, subgen. 189, 191
Lastreopsis 185
Leptorumohra 185, 186, 197, 198
Lithostegia 185
Lomariopsidaceae 184
Lophodium 187
foenisecii 195
multiflorum 187, 195

Nephrodium 184, 187
marginale 187
monticola 192
Nothoperanema 185, 186, 195, 207

Onocleaceae 184

Peranemaceae 184
Peranemataceae 184, 185
Phanerophlebiopsis 186
Phegopteris 188
Polypodiaceae 184
Polypodium 188
filix-mas 188, 189
Polystichopsis 188
Polystichum 185, 188, 193, 195
Psidopodium 187
Pycnopteris 188, 189
sieboldii 188, 189

Rumohra 185, 186, 188
Acrorumohra, sect. 186, 197, 198
adiantiformis 185
aspidioides 185

Stenolepia 185
Stigmatopteris 185

Tectaria 184
Thelypteridaceae 184

Woodsiaceae 184

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Ferns of Jamaica
A guide to the Pteridophytes

G. R. Proctor

This flora records and describes the 579 species and 30 varieties of ferns occurring in Jamaica. The succinct species descriptions include relevant synonymy and incorporate distributional data both within and outside Jamaica. Special emphasis is given to the subtle distinctions between closely related species and all genera are illustrated. Keys to the genera and species facilitate a wider use of the flora in the West Indies and northern South America. The author, one time Senior Botanist in charge of the Herbarium of the Science Museum, Kingston, Jamaica, is an outstanding field botanist and his expertise is reflected in the practicality of the flora and especially in the habitat and ecological information. This volume represents an important addition to our knowledge of the flora of the West Indies.

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NATURAL HISTORY

Evolutionary cladistics of marattialean ferns

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Contents

Synopsis 219
Introduction 221
I. Taxonomic relationships 222
  Methods 222
    Method of cladogram construction and introduction to terminology 222
    Choice of terminal taxa 226
    Choice of outgroups 227
    Observation of characters 228
    List of characters 228
    Excluded characters 231
    Discussion of characters 233
  Results and discussion 266
    Comparison of the cladogram with previous classifications 266
    Definition and relationships of the internested taxa 272
    Identity of *Psaronius* + *Scolecopteris* 276
    Definition of genera of extant Marattiales (Marattiaceae) 276
    Provisional written classification of Marattiales 278
II. Phylogenetic relationships (evolutionary cladistics) 278
  Introduction 278
    Principles of evolutionary cladistics (sequence analysis) 279
    Argumentation for invoking a time axis 281
    Stratigraphy of relevant fossils 282
    Biogeography 285
    Ontogeny 288
    Ecology and comparative physiology 290
  Conclusions 291
Summary 291
Taxa and specimens studied 292
Acknowledgements 294
References 294

Synopsis

A new classification of the marattialean ferns is proposed, based on an overview of the characters of extant species compared with Ophioglossales and the fossil Psaroniaceae. The new classification shows considerably greater resolution of taxonomic relationships than previously proposed classifications, of which the scheme most widely adopted had no resolution of relationships and was therefore totally uninformative. The new scheme is not only relatively informative taxonomically, but is also consistent with independent evidence from ontogeny, biogeography, and stratigraphy of fossils. This was either not the case or was at best scarcely so with the previous classifications. The general principles for testing phylogenetically interpreted cladograms utilising independent evidence ('evolutionary cladistics' or 'sequence analysis') are discussed.

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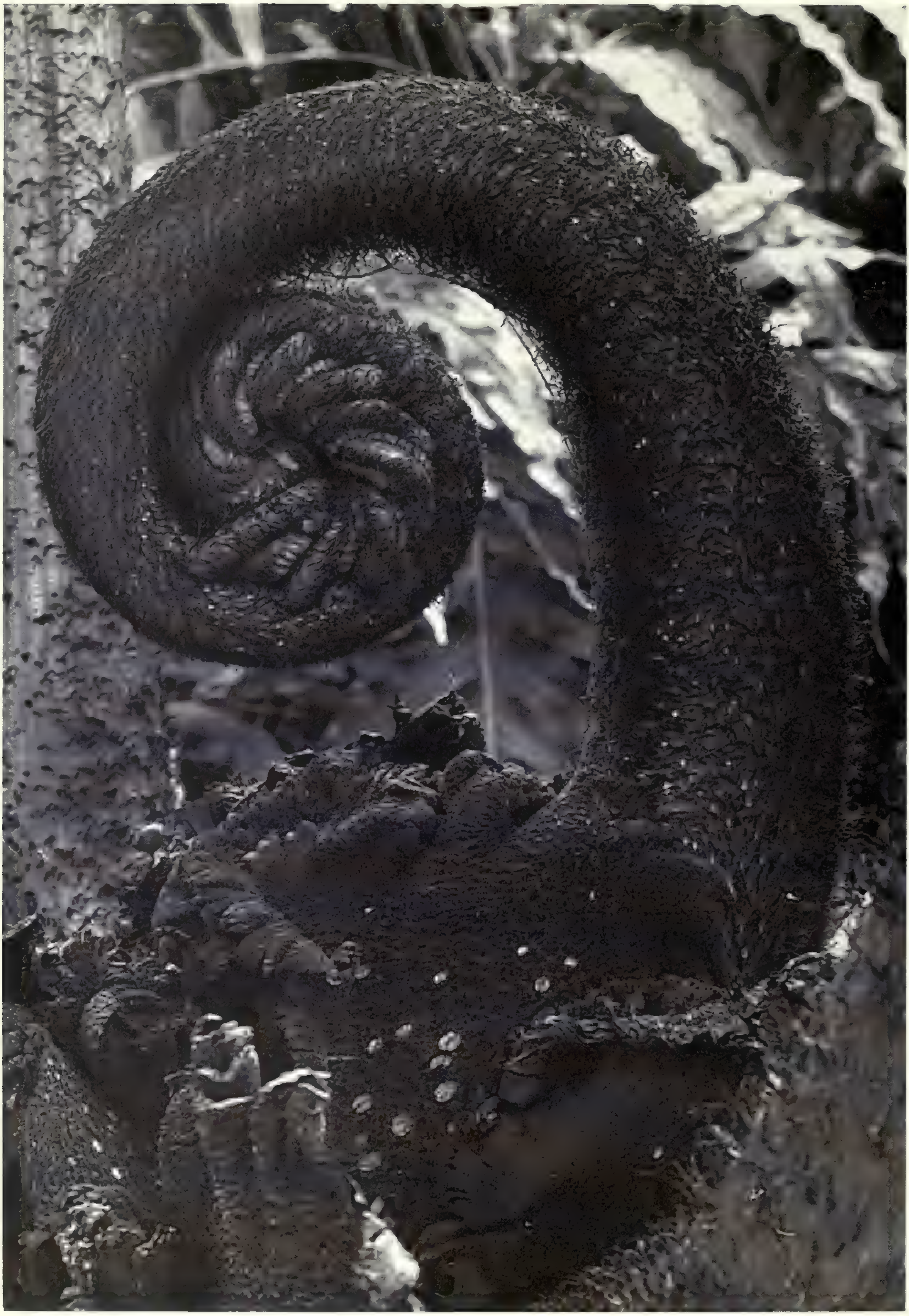

Introduction

In his incisive survey of ferns, Edwin Bingham Copeland (1947) drew attention to their unsatisfactory classification at ranks higher than the genus, particularly at family rank. Marattiales is no exception. At least nine family classifications have been proposed for the order in the past, of which the one embraced by most authors (Fig. 25A) is totally uninformative. It merely groups the seven extant genera into the order as a whole, with no further subdivision. Such a classification is uninformative because it fails to indicate relationships.

This paper provides a general overview of extant Marattiales prior to more detailed taxonomic revision and is mainly about relationships. It concerns them in two senses, firstly (in part I of this paper) in terms of classification (taxonomic relationships), secondly (in part II) in a wider, explanatory context, in terms of evolutionary history (phylogenetic relationships). To evaluate *taxonomic relationships* we use the now well-established method of biological classification termed cladistics. Cladistics is preferred to other methods of classification, such as phenetics, because for certain purposes it is superior to them: it has a greater potential for unambiguous definition of higher taxa and it has in particular a greater potential for detailed resolution of their relationships. Thus we provide a classification of Marattiales that enhances understanding of generic and higher taxonomic limits for this group and that has a demonstrably greater resolution of ranks than any previous classification.

One of many aspects of these ferns requiring further study is the need for a more appropriate circumscription of the genera. This is briefly discussed and attention is drawn to the complex relation between methods of classification and pragmatic considerations of taxonomic judgement: cladistics in our view has considerable value in this regard but should not be misunderstood. It has limits and provides a no more universally practical system for delimiting genera and species than any other method of classification. The most important taxonomic use of cladistics is for defining taxa at ranks higher than the genus and for assessing their relationships.

In terms of *phylogenetic relationships* the Marattiales are of special interest. Not only are they the most primitive filicopsids surviving today, but also they are well represented by fossils from Palaeozoic times onwards. This makes them an ideal subject of study from the explanatory viewpoint of evolutionary history and relationship. The great resolution of taxonomic (particularly internested) relationships provided by cladistics is of particular relevance in this regard. In the context of general evolutionary theory such relationships may be interpreted as predicting relative ages of origin of the taxa. We show that these predictions for Marattiales, based in part on studies of the characters of living genera, are in fact corroborated by the relevant fossil (stratigraphic) evidence. Such evaluation of independent fossil evidence could not even be contemplated from the uninformative classification formerly so widely adopted, which, interpreted in these terms, implied that all extant species of Marattiales arose at the same time. Indeed it is precisely such a consideration, set in the broader context, that makes cladistics of much greater empirical value than merely an alternative method of classification.

Whilst Marattiales therefore provides an example for promulgating the theory and practice of evolutionary cladistics, these ferns are also inherently challenging. Although widely discussed at textbook level (Bierhorst, 1971; Eames, 1936; Copeland, 1947; Sporne, 1975) they are poorly known at the research level. As plants of tropical and warm temperate environments and therefore under some threat of extinction, this is particularly unfortunate. Thus, although we aim here mainly to provide an overview of the group, a number of new observations have been made. These range from characterisation of such features as the intercellular rods that occur on the walls of the spongy mesophyll cells to preliminary consideration of a possibly new species of *Danaea*, which is remarkably similar in habit to the Carboniferous fossil *Psaronius*. In addition some persistent errors are corrected, for instance the assertion that the walls of marattialean sporangia have stomata (Sporne, 1975).

Definition of extant Marattiales has hitherto been rather vague, but their often huge size (with

Frontispiece Crozier of *Angiopteris evecta* (G. Forster) Hoffm. *C. D. Sayers* 4, New Guinea (K. hort. 723–63.72306). ×*c*.0·7.

the fronds of some species up to 7 m long being the largest of any fern), pulvini of the fronds and peculiar fleshy stipules at the base of the stipe, are well known (e.g. Copeland, 1947, Sporne, 1975), as in particular are the synangia of the genera *Christensenia* Maxon, *Danaea* Smith, and *Marattia* Swartz. *Christensenia* is limited in its geographic distribution to tropical forest clearings in south-east Asia and, with its 'palmate', reticulate-veined fronds, rounded synangia, and huge stomata (the largest of any vascular plant), it differs markedly from all other genera. The fronds of the other genera are pinnate with open venation and have elongate synangia or sori. *Danaea*, known only from the western hemisphere, has synangia deeply sunken in the lamina tissue, whereas the only pan-tropical genus, *Marattia*, has the synangia borne on the surface of the lamina, as is characteristic also of all the other genera (sometimes borne on a pedicellate placenta in this genus). The remaining genera, *Macroglossum* Copeland, *Angiopteris* Hoffmann, nom. cons., *Archangiopteris* Christ & Giesenhagen, and *Protomarattia* Hayata are limited in their distribution, like *Christensenia*, to the eastern hemisphere. All are normally free-sporangiate (i.e. objectively with true sori when mature), though those of *Protomarattia* show fusion of the dorsal walls of the sporangia so as to be partly synangiate.

In summary, the aims of this study are 1. To assess the taxonomic relationships of extant Marattiales using cladistic method. 2. To compare this assessment with previous classifications, especially regarding previous family classifications and also with preliminary reference to generic circumscription. 3. To assess taxonomic relationships in general evolutionary (i.e. phylogenetic) terms of descent with modification, with reference to stratigraphic, ontogenetic, and biogeographic evidence provided both by the extant and the fossil members of the order. Brief reference is also made to the importance of ecological evidence in an evolutionary context.

I. Taxonomic relationships

Methods

Method of cladogram construction and introduction to terminology

This section is intended to introduce some basic concepts and terms for readers unfamiliar with cladistics. It is not intended to be a comprehensive summary, and fern workers wishing to learn more about the method should study Wiley (1981), Hill & Crane (1982), and Hennipman & Roos (1982, 1983). Readers already familiar with cladistics should start at p. 226.

The method of *cladistics*[1] in the strict sense used here and also by most other workers today is entirely comparative: it is based solely on taxonomic characters and excludes reference to biogeography, ontogeny, or stratigraphy (see Hennig, 1966), though many authors still make some reference to ontogeny (e.g. Wiley, 1981; Hill & Crane, 1982) and to some extent this is unavoidable. The main object of the method is to produce a hierarchical classification in which taxa are defined by characters shared uniquely by their members and so far as possible not shared with any other taxon. In logical terms (Hill, 1981) the subclasses in the classification hierarchy are defined both necessarily and sufficiently by their characters, so that these

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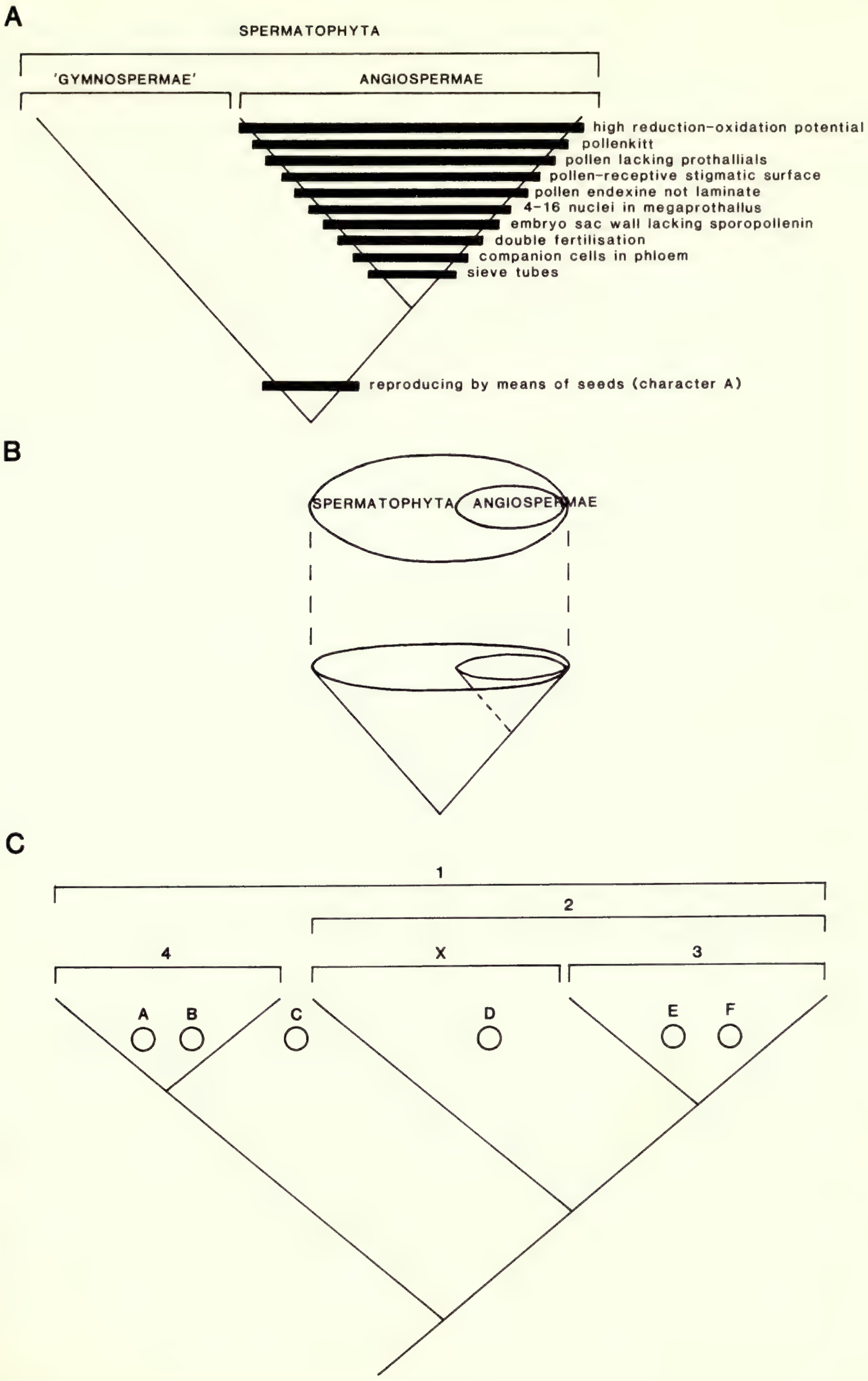
[1] Cladistics may be defined as a method of hierarchical biological classification in which groups are defined so far as possible only by reference to characters that distinguish a group from all others and that are shared by every member of the same group. For instance, the group 'Seed plants' encompasses all plants that share the character of the life-cycle 'reproducing actually or potentially by means of seeds'.

Fig. 1 **A**, Cladogram showing the relationships and defining characters (synapomorphies) of the cladistically natural taxa Spermatophyta and Angiospermae. Synapomorphies are shown as black bars. Synapomorphies abbreviated from Hill & Crane (1982), Hesse (1980, 1984) and Kubitski & Gottlieb (1984). The taxon 'gymnospermae' is not cladistically valid. It is a paraphyletic (grade) group. **B**, Diagram in three dimensions to show the same relations in terms of class inclusion. The subclass Angiospermae is internested within the more inclusive class Spermatophyta. Diagram **A** may be thought of as a vertical section of diagram B. **C**, Diagram showing relations of internesting of taxa. The relations of taxa 1, 2 and 3 are of class inclusion, i.e. of internesting, as is that of 4 to 1. The relation of taxon 4 to 2 or 3 is not an internested relation and cannot be compared in such terms. A–F are the individual members of taxon 1 and its various included sub-groups 2–4. Segment X is a paraphyletic taxon. Taxa 1–4 are cladistically natural.


A
SPERMATOPHYTA
'GYMNOSPERMAE'
ANGIOSPERMAE
high reduction-oxidation potential
pollenkitt
pollen lacking prothallials
pollen-receptive stigmatic surface
pollen endexine not laminate
4-16 nuclei in megaprothallus
embryo sac wall lacking sporopollenin
double fertilisation
companion cells in phloem
sieve tubes
reproducing by means of seeds (character A)
B
SPERMATOPHYTA
ANGIOSPERMAE
C
1
2
4
X
3
A
B
C
D
E
F

characters in principle are individually sufficient for group definition[2]. Such characters are commonly termed *synapomorphies* (Hennig, 1965, 1966). Examples of cladistically valid, i.e. *cladistically natural*, taxa (Fig. 1A) are the taxon Seed Plants (Spermatophyta), which is defined uniquely as a taxon by the capacity of all its members to reproduce by means of seeds; and the Flowering Plants (Angiospermae), defined by at least ten uniquely shared characters, for instance double fertilisation and the occurrence of axially aligned companion cells in the phloem, derived during development from the same mother cells as the sieve elements (Hill & Crane, 1982, give eight of these ten Angiosperm synapomorphies, for the other two cited here see Hesse (1980, 1984) and Kubitzki & Gottlieb (1984)).

Within the seed plants, the gymnosperms ('Gymnospermae') provide an example of a cladistically unnatural taxon. Gymnospermae is considered unnatural because these plants possess no uniquely shared characters (Fig. 1A). The group is only definable on a *phenetic* basis, by a combination of characters of two types: a) a character shared with other taxa, in this example with Angiosperms, i.e. character A, the capacity to reproduce by means of seeds; and b) characters that are lacking compared to such other taxa, i.e. the lack of all ten of the synapomorphies of Angiosperms. In other words, gymnosperms are plants that reproduce by means of seeds but do not have double fertilisation or companion cells in the phloem, and so on. Or still more plainly, such groups can be defined as groups only by a combination of the characters they have and those they do not have, and even the characters they have are not unique to them, such that the characters can only collectively be sufficient for group definition. Other botanical examples of such non-cladistic ('grade' or *paraphyletic*) taxa often referred to in current literature are cyanobacteria, psilophytes, rhyniophytes, trimerophytes, pteridophytes, progymnosperms, pteridosperms, proangiosperms and dicotyledonous Angiosperms (Bremer & Wanntorp, 1978; Hill, 1981*a*; Hill & Crane, 1982; Crane & Hill, in press; Hill, in preparation; Crane, in preparation).

Characters such as character A of the gymnosperms, referred to above and in Fig. 1A, are too generalised in their distribution to function as synapomorphies at the rank in question (i.e. of gymnosperms) and are termed *plesiomorphous* or *plesiomorphies* (Hennig, 1965, 1966). Plesiomorphies are of no value in defining cladistically natural groups because they are characters applied at an inappropriately low rank, i.e. at too low a rank in the classification hierarchy to uniquely define a group. Whilst character A functions as a clear synapomorphy at the more inclusive rank of Spermatophyta (Fig. 1A), it is too generalised in its distribution to be cladistically valid for defining any particular sub-group such as gymnosperms or Angiosperms: it simply becomes redundant at these ranks for cladistically valid definition of those taxa and, at these ranks, is therefore a plesiomorphy.

A cladistic classification is logically best expressed in a diagram that is three-dimensional (Fig. 1B) but for practical purposes is generally expressed diagrammatically in two dimensions as a dichotomously forking diagram termed a *cladogram* (Figs 1A, 23). Cladograms sensu stricto explicitly show a) the synapomorphies used to define the cladistic taxa and b) the *taxonomic relations* of the taxa, i.e. the pattern of and extent to which they form *internested sequences* (in Figures 1A and B the taxon Angiospermae is *internested* within the more inclusive taxon Spermatophyta). Such diagrams may also be summarised in written form (Eldredge & Cracraft, 1980; Wiley, 1979, 1981), in which case the synapomorphies themselves are in general no longer shown, though the internested relations of the taxa are carefully preserved by means of certain conventions (see Wiley, 1981 for a comprehensive account).

It follows from the definition of cladistics given above that production of a cladogram involves a) observation of characters and b) an assessment of their relevance as synapomorphies. (This means that what is initially 'observed' to be a character may, after study, in some cases later cease to be recognised as a character, or at any rate as one of cladistic relevance. Platnick (1979: 542–543) comments appropriately that cladistic characters (synapomorphies) as such are not

[2] In practice cladistics is not quite so simple, owing to the widespread occurrence of homoplasies and also to interpretative difficulties that can occur in recognising which characters are cladistic homologies (synapomorphies). The sentence in the text assumes, therefore, that characters have been diagnosed correctly as synapomorphies. For pertinent discussion of the use of characters in cladistics the reader is referred to Platnick (1979: 542–543).

observable as 'given' but are empirical, i.e. theory-laden, properties.) An important additional requirement is appropriate selection of the taxonomic units to be compared. These may range from subspecies to higher taxa, depending on the problem in hand, yet they are in each case (regardless of their rank) the lowest rank to be analysed. They are therefore generally termed *terminal taxa*, since they occupy the ends of the 'branches' of the cladogram and are of variable rank. They are equivalent in function to the *operational taxonomic units* of some authors (e.g. Sneath & Sokal, 1973) and are not necessarily themselves definable by having unique (*autapomorphous*) characters, though many cladists insist on this requirement (see Hennig, 1966 vs Wiley, 1981; Hill & Crane, 1982; 308–310 and this paper p. 277 for a range of views). The choice of terminal taxa for Marattiales is discussed below.

Assessment of the relevance of characters as synapomorphies requires study of the *distribution* of characters amongst the terminal taxa selected. If two or more terminal taxa uniquely share the same character, that character is potentially a synapomorphy. As will be evident from Fig. 1 and the foregoing discussion of it, synapomorphy and plesiomorphy are relative, one to the other, depending on the particular rank in the hierarchy. Equally, vice versa, a particular synapomorphy determines a particular rank (Hill & Crane, 1982). The main initial requirement in practice is therefore to determine the relative generality of the distribution of characters amongst the terminal taxa. For reasons given by, for example, Hill & Crane (1982: 275–280) and others, this is usually achieved by reference to a group having relatively more *generalised* (i.e. plesiomorphous) characters in comparison to the group being analysed. Such a group is termed an *outgroup* (Stevens, 1980; Wiley, 1981; Watrous & Wheeler, 1981). In the present study, the order Ophioglossales provides an outgroup for Marattiales as a whole, and the family Psaroniaceae (*Psaronius* + *Scolecopteris*) an outgroup for the extant Marattiales (as discussed below).

The class inclusion relation provides the logic behind hierarchical classification. It involves (by definition) the idea of *transformation*[3], from more general to less general characters in terms of their distributions. These characters respectively define more inclusive to less inclusive taxa, at respectively higher to lower ranks (Platnick, 1979). The inclusion relation necessarily involves hypotheses of polarity of characters into two or more *states*, from *character states* that are more generalised (−) in their distribution (relatively plesiomorphous character states) to those that are less generalised (+) in their distribution (relatively apomorphous character states). Determination of + vs − character states is based on the knowledge or assumption that most characters of the outgroup or outgroups relevant to establishing relationships are relatively generalised compared to those of the taxa being analysed in detail, in this case the extant Marattiales. Thus the spores of the outgroup Ophioglossales are typically round and trilete, the assumed − character state, whereas in some Marattiales they may be bean-shaped and monolete (regarded as the + character state).

In drawing up a cladogram the individual characters nearly always prove to conflict to some extent with others as potential synapomorphies. For instance character 66 (Table 2, Fig. 23) is uniquely shared by (and thus is potentially a synapomorphy of) a group composed of *Christensenia* + *Danaea* + *Marattia*, whilst characters 40 and 48 are (disregarding *Psaronius* + *Scolecopteris*) uniquely shared by, and therefore also potentially define, a group of *Marattia* + *Macroglossum* + *Angiopteris* + *Archangiopteris* + *Protomarattia*. These groupings are in conflict with one another over the appropriate higher taxon for *Marattia*. It could fit in either.

Because of such conflicts it is heuristically appropriate to select the cladogram that most economically (*parsimoniously*) represents synapomorphies. This is done with reference to the characters considered as a whole (Wiley, 1981; Hill & Crane, 1982: 281–2). Essentially, a taxon defined by three characters as synapomorphies would be preferred to one in conflict with it supported by only two potential synapomorphies. Such a choice may be made in practice (as in this study) by drafting up several alternative cladograms, totalling the number of conflicting characters in each case and finally selecting the diagram with the least number of conflicting characters: consistent, of course, with maximising taxa defined by synapomorphies. The residual conflicting characters, termed *homoplasies*, are indicated by asterisks in Fig. 23.

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[3] The term *transformation* here is used solely in a technical sense, such as that of mathematical transformations (in which, for instance, ellipses can be transformed into circles by decreasing the distance between the two foci). This meaning does not imply temporal transformation (see p. 281 for that different usage). Nor is the term used here in the same sense as Platnick (1979) in relation to schools of cladistic thought, though our views coincide with his (Platnick, 1979: 543).

Concentration on method of construction rather than on the aims of producing cladograms is not the main object of this paper (Feyerabend, 1978), and the foregoing is merely intended to briefly introduce terms and concepts for the general reader. However, it should be added that the method we have used (as with that of Hill & Crane, 1982) differs slightly from some others. Unlike *Compatibility* methods, for instance, (see e.g. Duncan, 1984) some of the data have not been initially discarded, though in the sense of minimising homoplasies (which represent potential synapomorphies) all methods eventually select from and to that extent exclude some of their data. Equally in the perceived interests of objectivity, our approach differs slightly from *Parsimony* method (e.g. Farris, Kluge & Eckhardt, 1970; Humphries, 1983; Churchill, Wiley & Hauser, 1984, 1985; Farris & Kluge, 1985). Unlike Parsimony method we have not treated characters which are near-synapomorphies, such as character 42, as if they were true synapomorphies of more inclusive taxa (of Marattiales as a whole for character 42) by invoking reversals. For this reason the resulting cladogram is overall probably somewhat less parsimonious than might be obtained by such method. Further work is in progress on these important details of method. The main thrust of the present paper, however, is different, and claims that the efficacy of the various methods for producing cladograms can only be assessed meaningfully for the biologist in the broader context of evolutionary theory, i.e. in the light of empirical evidence independent of that used to produce a cladogram.

Choice of terminal taxa

Although more than 300 extant species of Marattiales have been named, mostly in the genera *Angiopteris* and *Marattia*, a limited range of 23 species was selected to provide the terminal taxa for the cladogram. This selection was based on a background study of more than 150 named species and was designed to represent the main range of variation for each of the extant genera. For instance, although only five species of *Marattia* were selected (out of about 80 described species), these adequately represent the range of frond form and synangial structure for this genus (see Copeland, 1947, for relevant discussion). To cover the range of variation still more effectively, species at the boundaries of the genera as currently circumscribed were also selected besides those more characteristic of the genera; for example *Angiopteris monstruosa* Alderw. (intermediate between typical *Angiopteris* and *Macroglossum*) and *A. annamensis* C. Chr. & Tard. (intermediate between *Angiopteris* and *Archangiopteris*).

Apart from the 'filmy' species of *Danaea*, *D. trichomanoides*, the other named species of Marattiales studied but not shown in the cladogram differ in no important way for the purpose in hand than those selected. Indeed, as Christensen (1905) and Holttum (1978) remark for *Angiopteris*, the 200 or more species recognised by some authors have been regarded by others as a single variable species: in reality there may perhaps be between 10 and 30 natural species of this genus. Species discrimination in Marattiales has in the past been excessively fine. Species have been separated on minute details that almost certainly in most cases represent merely intraspecific variation within a relatively few evolutionary species. At present this can only, however, remain a matter of opinion, since detailed field and laboratory study is an essential requirement for proper understanding of the range of variation of characters within the whole plants and within populations. What is absolutely certain is that the fragmentary herbarium material of many of the type specimens, and the sometimes inadequate descriptions based largely or entirely on such material, means that many described species are of questionable value. The numerous named species of De Vriese in De Vriese & Harting (1853) and Ching (1959), for example, are mostly concepts applied, like the name, to fragments of fronds on herbarium sheets rather than to whole plants or populations of whole plants. Unlike the exemplary work of Holttum (e.g. 1978) no useful account is made of variation in the field or of cultivation under uniform conditions. A major problem is the large size of many of these plants: herbarium sheets are too small to individually represent the range of variation of pinna or pinnule form even within a single frond (often up to 7 m long!). Only a few collectors, notably A. H. G. Alston and C. J. Brooks, have tackled this problem realistically by collecting whole fronds and preserving them on an annotated series of sheets. As regards variation in the field and in populations raised in cultivation from spores, still less is known.

Some of our terminal taxa are probably unsatisfactory species, though we have tried as far as possible to use ones that are well circumscribed.

All the extant terminal taxa of Marattiales selected for the cladogram are species. However, the two outgroups Psaroniaceae and Ophioglossales are higher taxa. Information for the fossil Psaroniaceae (Stewart, 1983) was taken almost entirely from the literature. Several genera of fertile fronds and axes are now included in this family but we have limited our choice to the best known genera, *Psaronius* Cotta and *Scolecopteris* Zenker emend. Millay (1979). *Psaronius* is a genus of stem material attributed to the same whole plant as *Scolecopteris* (which is a genus of fertile frond material). We refer informally to the reconstructed fossil plant, which was a tree fern in habit, as *'Psaronius + Scolecopteris'*. Since there is considerable variation amongst the species of these genera there are several −/+ (◪) entries for them in the data matrix (Table 2) and cladogram (Fig. 23).

Choice of outgroups

Amongst extant plants the nearest outgroup to Marattiales is probably Ophioglossales (Bierhorst, 1971; Sporne, 1975). These plants are in some respects similar but in many are very different: for instance their 'aerial complexes' (Bierhorst, 1971) and exannulate sporangia, each sporangium having its own individual vascular supply, are more readily compared with 'trimerophyte' or 'aneurophyte' branching systems (Stewart, 1983) than with the laminate fronds and sori, composed of more or less annulate sporangia, possessed by most filicopsids. Nonetheless, they can be used as an outgroup for Marattiales as a whole, and so far as it is possible to assess homologies, we have referred to them as the main outgroup for the order. In relation to extant Marattiales however, Psaroniaceae is by far the most similar group, even though exclusively fossil. Although Psaroniaceae has a number of unique characters it has several generalised characters compared to extant Marattiales, yet is more closely related to them than to Ophioglossales by at least three characters of cladistic value. It may be regarded as a plesiomorphous sister group of Marattiales and thus as an outgroup (Stevens, 1980; Watrous & Wheeler, 1981). We have found Psaroniaceae of considerably more use than Ophioglossales in evaluating relationships amongst extant Marattiales.

We emphasise that Psaroniaceae is used as an outgroup purely in terms of character comparison: its Upper Carboniferous to Permian age is of no importance in assessing taxonomic relationships. Also, the range of characters used for the living genera has not in any significant way been narrowed to facilitate comparison with these fossils (cf. Patterson, 1981*a*).

An estimate of relative completeness of knowledge of characters of the fossil vs the living genera (*information gap index*) was calculated as follows. Using Table 2, the number of characters for *Psaronius + Scolecopteris* excluding those not applicable was totalled (69). This was divided into the number of characters for which information may potentially become known but which are at present unknown because of imperfect preservation (e.g. of root hairs) or incomplete study (e.g. the surface cell layer of the sporangium wall). Such characters for *Psaronius + Scolecopteris* in Table 2 are represented by blanks and total 9. Multiplication ×100 gives a percentage figure, the *information gap* for the fossil compared to its extant relatives: $9/69 \times 100 \simeq 13\%$ for *Psaronius + Scolecopteris*, a remarkably small gap. The position is considerably less favourable for other fossils discussed below, and for which therefore no formal inclusion in the cladogram has been attempted.

This index may equally be applied to lesser known extant species in comparison with better known ones. Thus for *Danaea* sp. A the index is currently $28/71 \times 100 \simeq 39\%$, for *Archangiopteris itoi* Shieh $16/69 \times 100 \simeq 23\%$ and for *Angiopteris elliptica* Alderw. $9/68 \times 100 \simeq 13\%$. These figures indicate that gaps in knowledge for some of the extant species may equal or even considerably exceed that for the fossil outgroup.

Observation of characters

Herbarium specimens have provided the main material and for many species were the only source of material for direct study currently available to us. As far as possible the type specimens were examined as well as other material of a species. The specimens studied for the cladogram are listed in the section 'Taxa and specimens studied', p. 292, others are indicated in the text. Observations on the dried material were supplemented both by spirit-preserved material at the British Museum (Natural History) (BM) and Kew (K), and with reference to live plants mainly at K, including *Macroglossum* which has recently been brought into greenhouse cultivation there. JMC was able to examine *Christensenia, Angiopteris* and *Marattia* in the field during a visit to Borneo in 1980.

Several methods were used to observe the anatomy of the herbarium specimens. The scales, frond hairs, and root hairs were removed and mounted in glycerin or gum chloral. Epidermal characters were examined by clearing pinnae or pinnules in a 10% aqueous solution of commercial bleach ('Domestos') for 6 to 24 hours, the exact time depending on ambient temperature as well as the resistance of the lamina to bleaching and the freshness of the bleach. After rinsing well in distilled water the preparations were stained with either gentian violet in ethanol or an aqueous solution of methylene blue. Surface details of synangia and sporangia were studied similarly, using 10% Domestos to bleach and restore them to the shape shown in life. (That the restored shape matches closely that in life was checked for a living plant of *Angiopteris* at K). After thorough rinsing the bleached material was stained with 1% safranin in ethanol and examined by optical microscopy. Sporangia and synangia were also examined in the air-dry and critical-point dried states using scanning electron microscopy. SEM was used to examine the projections on the walls of the mesophyll cells, and the spores (which were examined without acetolysis).

Sections of rhizome from the herbarium specimens were mostly made by hand-razor (in one instance requiring a hack-saw), and were stained with phloroglucinol + concentrated hydrochloric acid. Serial sections of fertile pinnules were made by microtome sectioning of herbarium material rehydrated in approximately 1% aqueous tri-sodium orthophosphate. Standard dehydration and infiltration procedures were used to embed the material in wax, staining with safranin and fast green or alcian blue. Sections were mounted in euparal.

Permanent slide preparations and the SEM stubs are in the Department of Botany, BM.

List of characters

This section lists the characters used to construct the cladogram of Marattiales shown in Fig. 23, using the method outlined above. For each character the character state considered to be relatively plesiomorphous (generalised) is given first, connected by an arrow (→) to the relatively apomorphous (less generalised) character state. This information applied to the terminal taxa selected for the cladogram is summarised in Table 2, which records the characters as − for the generalised state and + for the less generalised (derived) one. Where an entry for a character is not applicable this is indicated by /. For the reconstructed fossil plant *Psaronius* + *Scolecopteris* blank entries in Table 2 indicate characters for which information is as yet unknown owing to incomplete preservation or study. For the extant taxa, characters of this status are represented by a predicted state, which is indicated by enclosure within parentheses.

Several of the characters listed require explanation and discussion. This is dealt with on p. 233–266, preceded by a discussion of certain characters that were not used for the cladogram on p. 231–233.

1. *Stelar anatomy of adult stem*: solenostele → dictyostele.
   (Kuhn, 1889; Farmer & Hill, 1902; West, 1917*b*; Schoute, 1926; Chang, 1975; DiMichele & Phillips, 1977; Millay, 1979.)
2. *Number of cycles in dictyostele as seen in T.S. of adult stem*: one (monocyclic) – three (tricyclic) → more (polycyclic).
   (Kuhn, 1889; Shove, 1900; Farmer & Hill, 1902; Gwynne-Vaughan, 1905; Campbell, 1911; West, 1917*b*; Schoute, 1926; Stidd & Phillips, 1968; Chang, 1975; DiMichele & Phillips, 1977; Rothwell & Blickle, 1982; Mickle, 1984.)

3. *Meristeles in T.S. of adult stem*: in clearly visible cycles, distinct from a helix → cycles not clearly distinguishable from a helix.
(Kuhn, 1889; Shove, 1900; Farmer & Hill, 1902; Gwynne-Vaughan, 1905; Campbell, 1911; West, 1917*b*; Schoute, 1926; Morgan, 1959; Stidd & Phillips, 1968; Chang, 1975; DiMichele & Phillips, 1977; Rothwell & Blickle, 1982; Mickle, 1984.)
4. *Protophloem of stem meristeles*: external to the metaphloem (i.e. exarch) → internal to metaphloem (endarch).
(Shove, 1900; Brebner, 1902; Gwynne-Vaughan, 1905; Campbell, 1911; West, 1917*b*; Esau, 1969; Chang, 1975; Smoot & Taylor, 1981; Smoot, 1984.)
5. *Stipules borne in pairs at base of rachis*: absent → present.
(Christ & Giesenhagen, 1899; Hayata, 1919; Ching, 1958*a*; Morgan, 1959; Bierhorst, 1971; DiMichele & Phillips, 1977; Johns, 1981; Smoot & Taylor, 1981.)
6. *Pulvini in frond*: absent → present.
7. *Mucilage canals in stem*: absent → present.
(Kuhn, 1889; Gwynne-Vaughan, 1905; Campbell, 1911, 1914*b*; West, 1915; Stidd, 1971; Chang, 1975; DiMichele & Phillips, 1977; Rothwell & Blickle, 1982.)
8. *Mucilage canals in root*: absent → present.
(Kuhn, 1889; Gwynne-Vaughan, 1905; Campbell, 1911; Morgan, 1959; Chang, 1975; Ehret & Phillips, 1979.)
9. *Mucilage canals in axial components of frond*: absent → present.
(References as for character 8; also Brebner, 1902; Stidd, 1971.)
10. *Mucilage canals following course of lateral vein in lamina beneath sorus*: absent → present.
(Campbell, 1914*a, b*.)
11. *Sclerenchyma in stem cortex*: absent → present.
(References as for character 2, excluding Schoute, 1926, and including Goeppert, 1864–5; Kuhn, 1890; Brebner, 1902; Stidd, 1971; Smoot & Taylor, 1981.)
12. *Sclerified pith in stele of root*: absent → present.
(West, 1917*b*; Ehret & Phillips, 1977.)
13. *Continuous band of sclerenchymatous fibres in cortex of aerial or subterranean root*: absent → present.
(West, 1917*b*; Morgan, 1959; DiMichele & Phillips, 1977; Ehret & Phillips, 1977; Rothwell & Blickle, 1982.)
14. *Apparently sclerenchymatous cells occurring externally to cylindrical traces in stem or rachis*: absent → present.
(Shove, 1900; Brebner, 1902; Gwynne-Vaughan, 1905; Campbell, 1911; Morgan & Delevoryas, 1952*a, b*; Morgan, 1959; Stidd, 1971; DiMichele & Phillips, 1977.)
15. *Multicellular root hairs*: absent → present.
(Brebner, 1896; Campbell, 1911; West, 1917*a*.)
16. *Roots numerous and supported by parenchymatous tissue surrounding the mature stem at least towards its basal region*: absent → present.
(Morgan, 1959; Stidd & Phillips, 1968; Ehret & Phillips, 1977; Smoot & Taylor, 1981; Rothwell & Blickle, 1982.)
17. *Habit of adult stem*: erect → creeping.
(Mettenius, 1856; Campbell, 1911; West, 1917*b*; Morgan, 1959; Shieh, 1970; DiMichele & Phillips, 1977; Rothwell & Blickle, 1982.)
18. *Length of erect adult stem*: squat → elongate.
(References as for character 17.)
19. *Symmetry of adult stem*: radial or scarcely dorsiventral → dorsiventral.
(Shove, 1900; Campbell, 1911; West, 1917*b*; Morgan, 1959; DiMichele & Phillips, 1977; Rothwell & Blickle, 1982.)
20. *Extent to which mature fronds are pinnately divided*: 3 or more-pinnate → 2-pinnate.
(Stidd, 1971; Croft, pers. comm. 1983.)
21. *Extent to which mature fronds are pinnately divided*: 2-pinnate → 1-pinnate.
22. *Extent to which mature fronds are pinnately divided*: 1-pinnate → simple.
23. *Extent to which mature fronds are pinnately divided*: pinnate → palmate.
24. *More or less spiny transverse ridges on stipe of mature fronds*: absent → present.
25. *Soft spines on veins of pinnules*: absent → present.
(Stidd, 1971; Stidd & Phillips, 1980.)
26. *Stipe of juvenile frond*: without a pulvinus → with one pulvinus a short distance proximally to laminate region of frond.
(Christensen & Tardieu, 1935.)

27. *Stipe of adult frond*: without a pulvinus → with one pulvinus a short distance proximally to laminate portion of frond.
(Christ & Giesenhagen, 1899; Hayata, 1919, 1928; Ching, 1958*b*; Shieh, 1970.)
28. *Number of pulvini per stipe in adult frond*: never more than 1 → some fronds with 2 or more.
(References as for character 27.)
29. *Microscopic projections from exterior of walls of mesophyll cells*: absent → present.
(De Vriese & Harting, 1853; Luerssen, 1873*a, b*, 1875*b*; Schenk, 1886; Kuhn, 1889.)
30. *Stomata of lamina*: guard cells functional → permanently open.
(Campbell, 1911; Scott & Holden, 1933.)
31. *Stomata of lamina*: anomocytic or weakly cyclocytic → more or less strongly cyclocytic.
(Scott & Holden, 1933; Van Cotthem, 1970.)
32. *Stomata of lamina*: subsidiary cells typically dicyclic → typically dicyclic but with lateral subsidiary cells in a paracytic position.
(Van Cotthem, 1970.)
33. *Stomata of lamina*: subsidiary cells typically dicyclic → typically tri- or tetracyclic.
(De Vriese & Harting, 1853; Luerssen, 1873*a*; Van Cotthem, 1970.)
34. *Diameter of stomatal apparatus (excluding subsidiary cells)*: in general $< 80\ \mu m$ → in general $> 80\ \mu m$.
(Scott & Holden, 1933; Van Cotthem, 1970.)
35. *Anticlinal walls of ordinary epidermal cells (adaxial epidermis)*: more or less straight, curved or at most very coarsely sinuous → uniformly and markedly sinuous.
(References as for character 32, including Pant & Khare, 1969.)
36. *Idioblasts in abaxial epidermis*: absent → present.
(Christ & Giesenhagen, 1899; Van Cotthem, 1970; Ogura, 1972.)
37. *Lamina margin of pinnae or pinnules, excluding apex*: distinctly toothed or lobed → scarcely and inconspicuously toothed or lobed.
(Morgan & Delevoryas, 1952*a*; Millay, 1979, 1982*a, b*.)
38. *Fertile pinnae or pinnules*: barely recurved → recurved fully to protect sori.
(Morgan & Delevoryas, 1952*a*; Millay, 1979; 1982*a, b*; Stubblefield, 1984.)
39. *'Fibre' bundles alternating with and parallel to veins of lamina*: absent → present.
(Campbell, 1914*a*; Millay, 1979, 1982*a, b*.)
40. *Scales composed of*: more or less isodiametric cells → elongate cells.
(Scott & Holden, 1933; Stidd & Phillips, 1968; Stidd, 1971.)
41. *Depth of anticlinal walls of cells of scales, in scales with anticlinal walls more or less isodiametric as seen in surface view of the scale*: deep → shallow.
42. *Margin of scales*: more or less entire → lobed and/or fimbriate.
(Scott & Holden, 1933; Stidd, 1971.)
43. *Division of scale margin*: lobed → fimbriate.
44. *Uniseriate multicellular hairs on frond*: absent → present.
(Scott & Holden, 1933; Millay, 1979, 1982*a, b*.)
45. *Veins of lamina*: not normally reticulate → reticulate.
(Millay, 1979, 1982*a, b*.)
46. *Veins of lamina*: free to margin → anastomosing near margin to form a submarginal bundle.
47. *Sterile and fertile fronds*: monomorphic → distinctly dimorphic.
48. *Uniseriate multicellular branching hairs attached to placenta*: absent → present.
(Millay, 1979, 1982*a, b*.)
49. *Scales or hairs borne on synangial or sporangial wall*: absent → present.
(Millay, 1979, 1982*a, b*.)
50. *Tissue of lamina between sori*: scarcely expanded → expanded ¾ of the way up the height of the synangia or sporangia.
(Morgan & Delevoryas, 1952*a*; Millay, 1979, 1982*a, b*.)
51. *Placental tissue*: not incorporating tracheids → incorporating them.
(Luerssen, 1871–4, 1875*a*; Strasburger, 1874; Bierhorst, 1971; Millay, 1979, 1982*a, b*; Stubblefield, 1984.)
52. *Placenta*: without → with apparent epidermis.
(References as for character 51.)
53. *Placenta*: relatively weakly developed → relatively well-developed.
(Millay 1982*a*; Stubblefield, 1984.)
54. *Sporangia*: individually vascularised by one trace → sorus of several sporangia (or synangium) collectively vascularised by one individual trace.

55. *Arrangement of sori in ultimate divisions of frond*: two rows parallel to the midrib → approximately in two rows but rows parallel to the main lateral veins.
(Morgan & Delevoryas, 1952*a*; Millay, 1979, 1982*a*, *b*; Stubblefield, 1984.)
56. *Arrangement of sori in ultimate divisions of frond*: in two rows → relatively scattered.
57. *Position of sori relative to margin*: near to margin → midway between midrib and margin.
(Morgan & Delevoryas, 1952*a*; Millay, 1979, 1982*a*.)
58. *Symmetry of sorus in plan view*: in general radial → in general elongate.
(References as for 57, including Millay, 1982*b*; Stubblefield, 1984.)
59. *Spore-bearing loculi of synangia (or sporangia of sori) packed together*: loosely → closely.
(Millay, 1979.)
60. *Composition of surface cell layer of walls of sporangium or synangium*: all walls composed of more or less isodiametric cells → lateral (and ventral) walls of sporangium, or synangial septa between locules, composed of elongate cells.
(Millay, 1979, 1982*a*, *b*.)
61. *Alignment of cells of ventral wall of sporangium or synangium with dehiscence slit*: parallel → oblique.
(Millay, 1979, 1982*a*, *b*.)
62. *Group of more or less isodiametric, thick-walled cells at apex of sporangium or synangial locule*: absent → present.
(Millay, 1979, 1982*a*, *b*.)
63. *Number of sporangia or locules per sorus typically*: $> 10 \rightarrow < 10$.
(References as character 57, including Millay, 1982*b*; Stubblefield, 1984.)
64. *Ventral walls of opposing rows of sporangia or locules in the sorus*: free → adnate.
(Morgan & Delevoryas, 1952*a*; Millay, 1979, 1982*a*, *b*.)
65. *Ventral walls of sporangia or of locules of synangia*: laterally partially adnate → laterally free.
(References as for character 64.)
66. *Ventral walls of sporangia or of locules of synangia*: laterally partially adnate → completely adnate.
(References as for character 64.)
67. *Dorsal walls of sporangia or of locules of synangia*: laterally partially adnate → laterally free.
(References as for character 64.)
68. *Dorsal walls of sporangia or of locules of synangia*: laterally partially adnate → laterally completely adnate.
(References as for character 64.)
69. *Dehiscence of sporangia or synangial locules*: by longitudinal slits → pores.
(References as for character 64.)
70. *Shape and tetrad mark of spores (where visible)*: typically round and trilete → typically elongate and monolete.
(References as for character 64, including M. D. Crane, 1973; Millay, 1976; Stubblefield, 1984.)
71. *Exine ornamentation*: fundamentally granular or warty → with cones or spines.
(References as for character 70.)
72. *Exine ornamentation elements*: more or less free → commonly fused laterally, e.g. warts forming rugulae.
(References as for character 70.)
73. *Exine spines*: in general simple → bifurcating or further branched.
(References as for character 70.)

Excluded characters

Although we have attempted to study as many characters as possible, several have been excluded from the data matrix and cladogram, some because they proved too generalised (plesiomorphous) to be of use, such as the mesarch to endarch differentiation of protoxylem in the meristeles of the stem. This character state is shared with Ophioglossales and differs from the exarch maturation of most 'pteridophytes' (Ogura, 1972). In relation to 'trimerophytes' (which are centrarch) the condition in Ophioglossales and Marattiales is relatively derived but appears to be a grade character rather than one of genuine cladistic value, i.e. it is comparable to the gymnospermous xylem characters of 'progymnosperms', an unnatural group. This argument for exclusion applies in particular to the several generalised characters of the gametophyte, some of which are shared with bryophytes.

A few characters were considered but ultimately rejected because no sense could be made of them. One such character is the extent of elongation of the meristeles as seen in T.S. of the adult stem. Characteristically these form tangentially elongate bands in *Psaronius*, giving relatively few gaps per cycle whilst in extant Marattiales the meristeles are mostly strands, short in T.S. and generally with more gaps per cycle. However, the work of Morgan (1959) and others shows that although some species of *Psaronius* (e.g. *P. melanedrus* Morgan) have all the meristeles tangentially elongated, in some (e.g. *P. brasiliensis* Brongn. and *P. magnificus* (Herzer) Rothwell & Blickle) those of the inner cycles are of varied shapes and can be short (G. W. Rothwell, pers. comm.). It may also be noted that Mettenius (1864) records an interesting individual of *Angiopteris* that died after enduring unfavourable conditions of cultivation. The meristeles were almost continuous laterally in the upper part of its stem, as in *Psaronius melanedrus*.

A few characters were considered initially but later rejected through lack of uniformity of data. This applies particularly to biochemical information, mainly on flavenoids but also on a few other chemicals (e.g. Wallace, Story, Besson & Chopin, 1979; Wallace, Yopp, Story, Morris, Gomez & Stone, 1979; Wallace, Yopp, Besson & Choppin, 1981; Wallace, Markham, Giannasi, Mickel, Yopp, Gomez, Pittillo & Soeder, 1982; Richardson, 1984). It appears that *Marattia* and *Angiopteris* have been examined frequently but with only patchy reference to a few of the other genera, thus rendering this aspect at present of little use for the present study. Since herbarium material is in general adequate for such work, sampling could readily be made more representative in the future and we have sent samples to Dr M. Richardson with this in mind. The position is different for certain other kinds of information such as karyotype analysis, certain aspects of ontogeny, comparative ecology and physiology, and interbreeding behaviour. Knowledge of these for Marattiales is at present scanty, partly because live plants are an essential requirement for their study. Although chromosome numbers are known for all genera except *Archangiopteris* and *Protomarattia*, thorough karyological study has only recently been initiated. Interesting aspects of ontogeny remain unexplored, such as whether the sori are already developed in the crozier stage of frond development, whether the stipules can be understood as reduced pinnae, and the development of pulvini in the stipes of juvenile fronds of sporelings. Comparative physiological work is, so far as we know, at a primitive stage of progress on Marattiales, as also is experimental breeding and knowledge of their ecology.

With such longer-term possibilities in mind we are currently cultivating gametophytes of *Marattia, Macroglossum* and *Angiopteris*. Considering this against a background of continuing indigenous habitat destruction we have also attempted, with the help of colleagues, to bring representative material into greenhouse cultivation. *Marattia* and *Angiopteris* have been cultivated widely for a century or more, but other genera much less so. *Danaea* and *Christensenia* have been grown at K for some years, though optimum conditions for growth have yet to be achieved in this country and the plants remain at present entirely vegetative (*Danaea* has been grown successfully in N. America (J. M. Sharpe and J. E. Skog, pers comm.)). Recently, however, *Macroglossum* (collected by T. G. Walker and A. C. Jermy in 1978) has been very successfully cultivated at K, and from there is being actively distributed internationally. At the time of going to press, live plants of *Archangiopteris henryi* var. *somai* had just been received at BM from Taiwan, through the kindness of Tsai Linn-lai, and they appear to be growing satisfactorily at K. *Protomarattia*, which came from northern Vietnam and has not, to our knowledge, been collected for some 50 years, may well be extinct or almost so; if it survives, plants in cultivation would be scientifically invaluable. We should add that at any rate for species of large size, the small plants produced adventitiously on the stipules are usually sufficient for successful propagation of these ferns.

The character entries in parentheses in Table 2 indicate those for which the character state was merely predicted. Such instances, together with scant knowledge of their ecology, reveal a need for more thorough fieldwork on these plants than has formerly been the case (with the notable exceptions of collecting by A. H. G. Alston, C. J. Brooks, and R. E. Holttum). Sufficient information about the larger sized species has rarely been recorded (or material collected), and most existing herbarium specimens are mere fragments of the frond alone. These frequently give no information on even such basic characters as the outline of the lamina or degree of pinnation, nor of the stem, stipule and root form and structure. The internal tissue of the base of the stipe, and of the stipules and stem, is sometimes coloured a striking deep purple, a feature rarely noted by collectors. Thus its true extent cannot be judged exactly. This applies also to the extent of variation of characters from plant to plant within a stand, and from stand to stand. Only such work, combined with cultivation under uniform conditions and study of variation in sporelings, is likely to reveal the true extent of intraspecific variation and thus to assist in verisimilitudinous discrimination of species-level differences. Evolutionary study (as opposed to speculation) in a Darwinian (adaptationalist) context is precluded without a sophisticated knowledge of physiology and ecology.

Discussion of characters

This section refers to characters requiring explanation and discussion for several reasons: (*a*) of observations that are new; (*b*) where accounts in the literature are scattered and in some cases confused, and thus in need of synthesis or correction; (*c*) where our choice of polarities of the character-states requires clarification, particularly in comparison with the outgroups *Psaronius* + *Scolecopteris* and Ophioglossales; (*d*) to set the 23 terminal taxa chosen for the cladogram into the context of the broader sample of species studied as background material. The object of the discussion is to attempt to clarify exactly what we have done and thus to facilitate criticism and improvement by others in the future (Stevens, 1980).

1. *Stelar anatomy of adult stem.* Despite the work of Beck, Schmid & Rothwell (1983) and Schmid (1983) in the United States and of Sporne (1975) in England there is as yet no single clear system for classification of all steles of vascular plants. Sporne's system is in general simpler, it is more explanatory in biological terms and to that extent is preferable, but the American system is easier to apply as a classification in certain instances. The work of Kuhn (1889), Farmer & Hill (1902) and West (1917*b*) suggests that the stele of *Christensenia* may best be described as a perforated solenostele sensu Sporne (Ogura, 1972, refers to it as a dictyostele), though further work is needed.

Steles of adult stems of Ophioglossales are variable and mostly defy straightforward classification but may be considered to range from medullated protosteles through a solenostele to rudimentary perforated dictyosteles sensu Sporne (Bierhorst, 1971; Ogura, 1972: 285–7; Sporne, 1975). Millay (1979: 55–56) discusses *Psaronius* which also has a wide range of stelar anatomy. The range of adult stelar anatomy of the stem in Ophioglossales, *Psaronius* and extant Marattiales is similar in each taxon, though the occurrence of simple medullated protosteles in *Botrychium* (which we consider the most plesiomorphous genus of Ophioglossales) suggests that the simpler steles should be considered plesiomorphous in these taxa. This polarity is consistent with ontogenetic evidence. The alternative, however, that a dictyostele is the generalised condition for Marattiales (with consequent reversal to a solenostele in *Christensenia*) cannot be entirely excluded as a possibility. This polarity might well be selected by Parsimony method.

2. *Number of cycles in the dictyostele as seen in T.S. of adult stem.* Information on this and other characters of the stem is meagre because stems of the larger sized plants, the size of barrels, are rarely collected. Living material in cultivation is so scarce that few plants have been sacrificed for anatomical study. The few anatomical observations that have been made, published some time ago, are of limited use because the ontogenetic stages of the individuals studied were varied and the exact stage was rarely specified. This provides a poor basis for comparison of equivalent developmental stages, termed *semaphoronts* (Hennig, 1966) and which is a basic requirement of cladistics. In some of the early studies only young stages were examined, for example of *Macroglossum* (Campbell, 1914*b*) and *Marattia alata* Sw. (Charles, 1911).

Gwynne-Vaughan (1905) and Chang (1975) examined stems of *Archangiopteris henryi* Christ & Giesenh., and Hayata (1928) illustrated the vascular system of *A. henryi* var. *somai* (Hayata) Tagawa (under the name of *Protangiopteris somai* Hayata). Each study shows a monocyclic dictyostele but with an 'internal strand' (Gwynne-Vaughan, 1905) or 'connecting vascular bundle' (Chang, 1975). These steles are treated here as monocyclic (i.e. dictyosteles sensu stricto of Schmid (1983)), although clearly incipiently dicyclic.

Sectioning of the apparently new species of *Danaea* referred to in this paper as *Danaea* sp. A (Figs 2, 3), revealed a dicyclic stele (Fig. 4A).

The steles of adult stems of Ophioglossales are never more than monocyclic and thus they provide an unambiguous basis for the polarity adopted here. Their occasional internal strands of xylem tissue are considered to be of no biological significance (Ogura, 1972: 287).

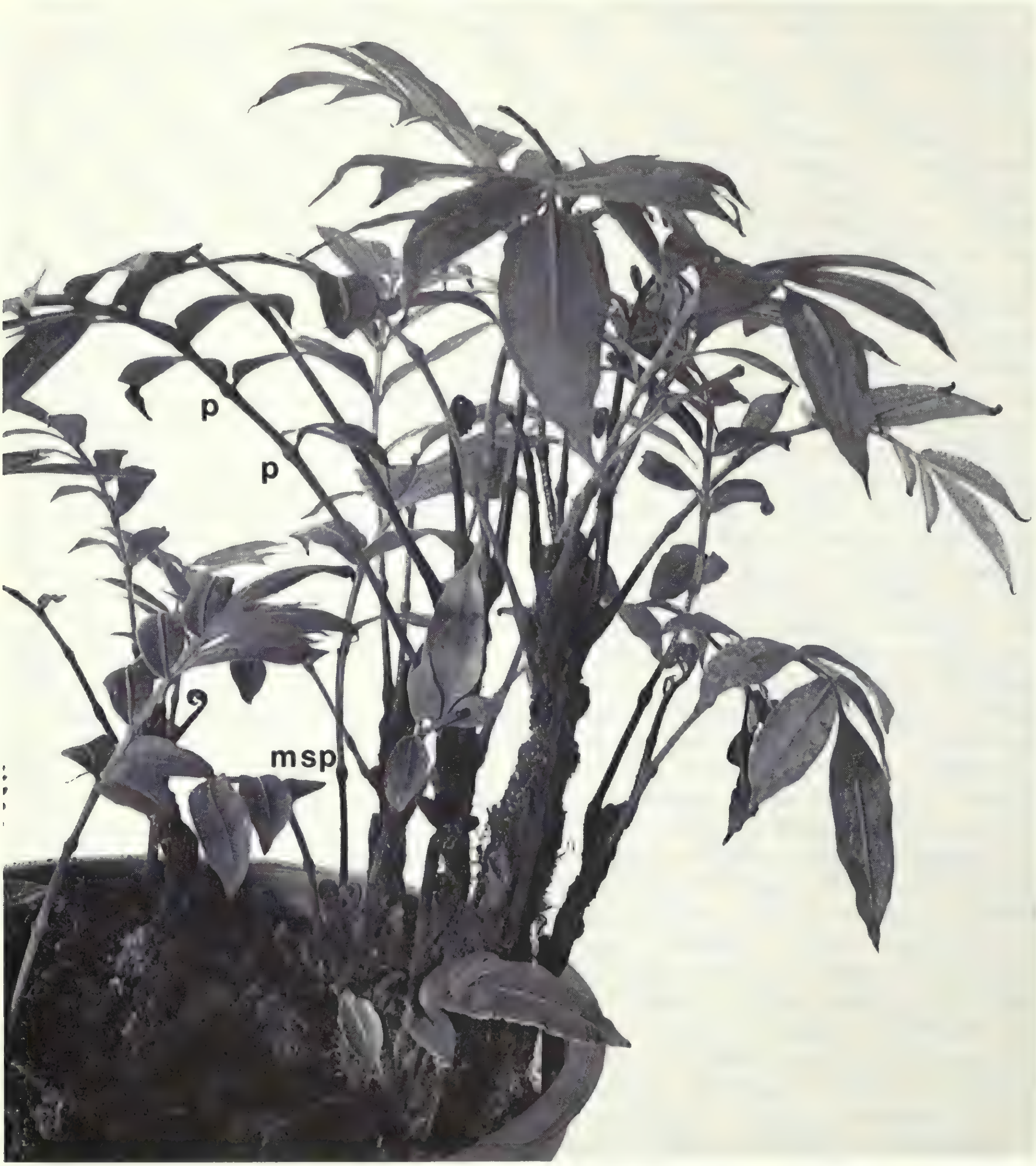
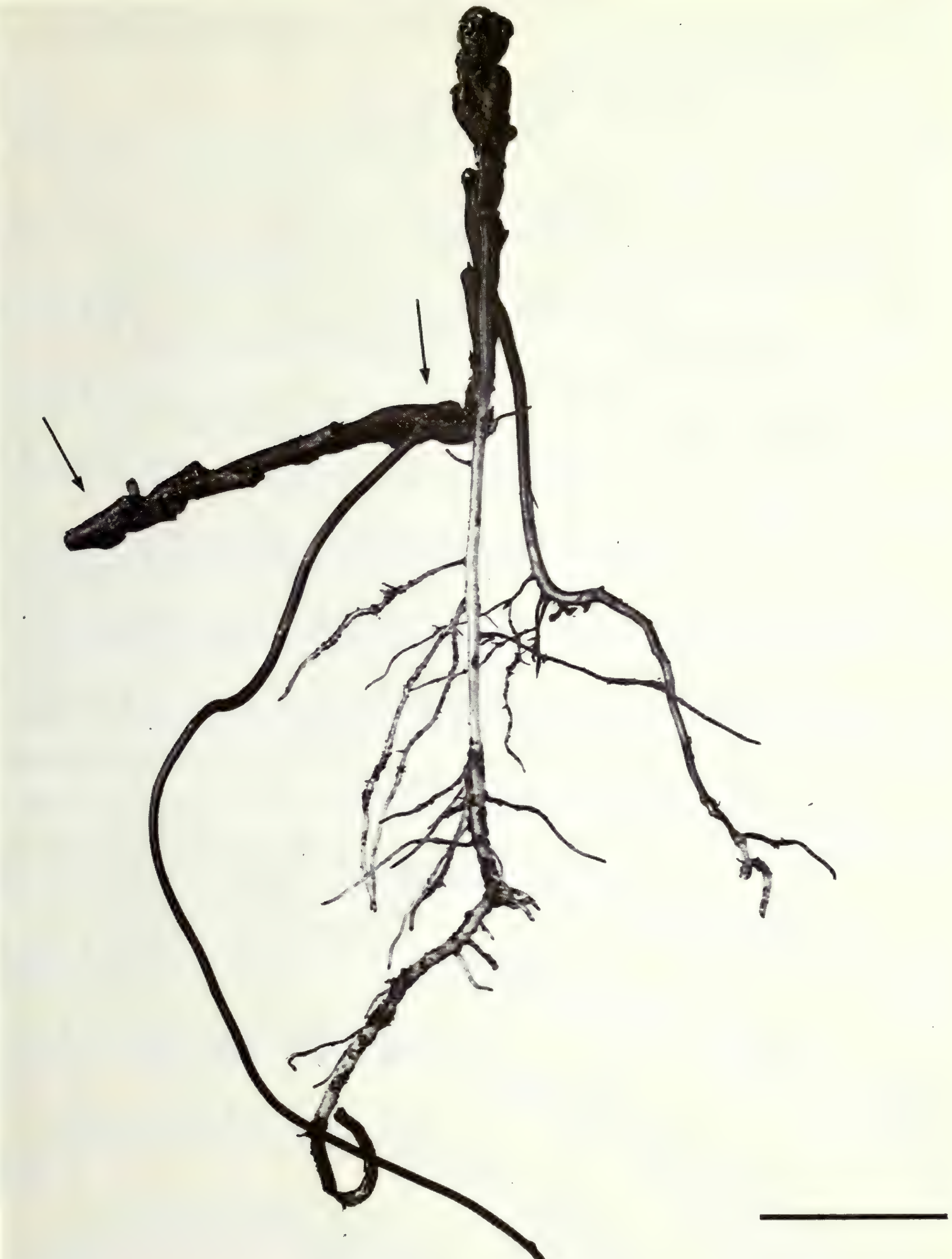


Fig. 2 *Danaea* sp. A., *P. J. Edwards & J. R. Woodhams* KER 1026, Guyana (Kew hort. ref. 174–78.01484): showing erect growth habit, pulvini (p, character 6), and mid-stipe pulvini (msp, character 28). × 0·5.

Fig. 3 *Danaea* sp. A., *P. J. Edwards & J. R. Woodhams*, KER 1026, Guyana (BM pteridophyte spirit collection B.72, Kew hort. ref. 174–78.01484): showing aerial production of roots. The horizontal part of the stem (arrowed) is the original portion collected in Guyana where it grew erect. It was pinned horizontally on the soil surface by the gardener at Kew. The new growth resumed the erect habit. Scale bar represents 5 cm.



3. *Meristeles in T.S. of adult stem.* The monocyclic steles of Ophioglossales could hardly be otherwise than cyclic and thus are not considered applicable for determining polarity of this character. *Psaronius* + *Scolecopteris* is therefore used as the outgroup.

4. *Phloem maturation of stem meristeles.* In Ophioglossales, protophloem cannot usually be distinguished from metaphloem but where evident it is exarch as in most other 'pteridophytes' (Esau, 1969; Ogura, 1972). The endarch phloem maturation of Marattiales is therefore considered apomorphous compared to the outgroup.

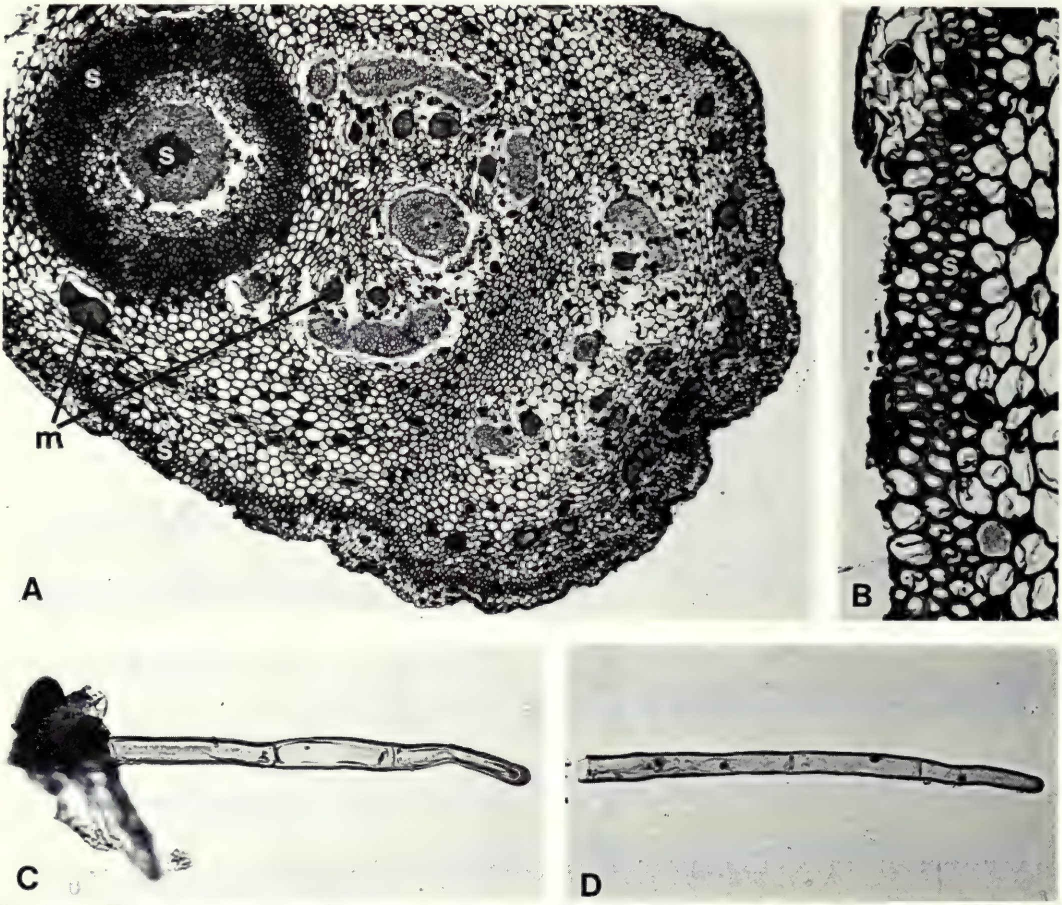
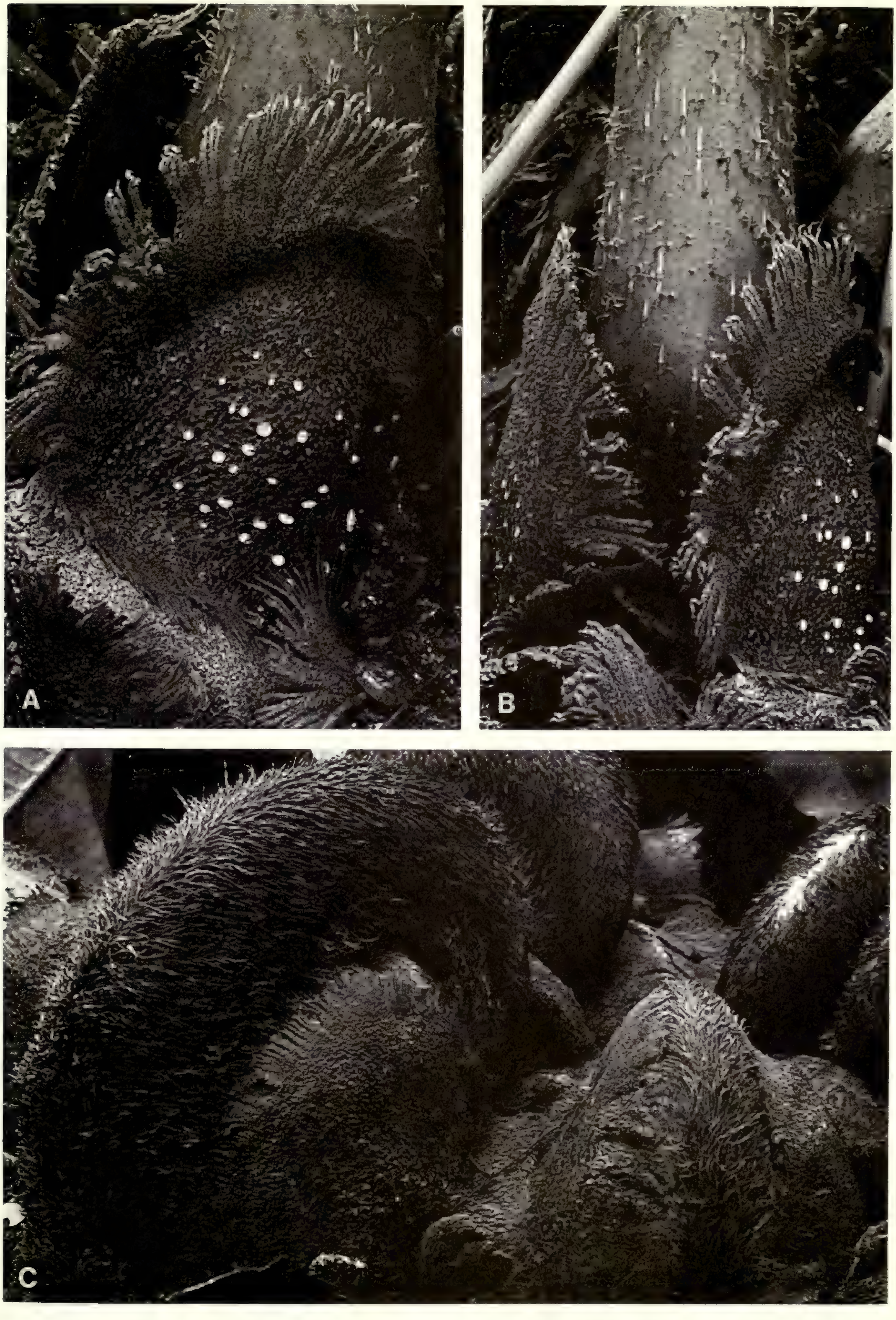


Fig. 4 **A**, Transverse section of stem of *Danaea* sp. A., *P. J. Edwards & J. R. Woodhams* KER 1026, Guyana (BM pteridophyte spirit collection B.72, Kew hort. ref. 174–78.01484): dicyclic dictyostele (character 2) in centre, with meristeles of outer cycle in short arcs, mucilage canals (m, character 7), sclerenchyma in hypodermal layer of stem (s, character 11), in root pith (s, character 12) and in root cortex (s, character 13). Traces to a frond are visible at right. × 12·5. **B**, Detail of A to show sclerenchyma in hypodermal layer of stem (s, character 11). **C**, **D**, *Danaea alata* Smith, *A. C. Jermy* 10936, Trinidad (BM): multicellular root hairs (character 15). D shows the nuclei clearly. C × 150, D × 120.

Fig. 5 Stipules of extant Marattiales (character 5). **A**, **B**, *Angiopteris* sp., *A. Paterson* 362, Sumatra (K. hort. 118–74.01395): showing shape of the stipules, their fimbriate-lacerate margin and lenticels. Note also the elongated lenticels on the frond stipes. A also illustrates the broad base of the stipules, and B the pair of stipules clasping the swollen basal region of the rachis. A × *c.*0·70; B × *c.*0·75. **C**, *Angiopteris hypoleuca* Vriese, origin unknown (K. hort. 000–73.13071): stipules intimately shielding the unfurled laminate region of young fronds. In this species, at the stage of frond development when photographed, the abaxial and lateral regions of the rachis were left exposed. Note the differently divided margin and surface texture compared to the stipules in A and B. × *c.*0·85.


A
B
C

5. *Stipules* (Fig. 5). These are expanded flap-like organs attached in a pair to the stem at the extreme base of each rachis. On anatomical grounds they are considered to be part of the frond (Bierhorst, 1971). Their shape is orbicular to oval, attached by a broad base (Fig. 5A). Numerous vascular traces enter the base and, where clearly seen (e.g. in *Danaea*) they run parallel (with slight divergence from one another) to the margin. Such venation may be described as approximately cyclopteroid but details are poorly known. The free margin of the stipules ranges from more or less entire to uniformly fimbriate (Fig. 5C); sometimes it is more unevenly divided (Fig. 5A, B), and may be divided into broad lobes or even become broadly crenulate (Frontispiece). The divisions are never very deeply incised. Further work on the range of stipule form and structure of extant Marattiales is in progress.

In the young crozier the stipules intimately clasp the unfurled laminate region of the frond, sometimes leaving the abaxial and lateral region of the rachis exposed (Fig. 5C). They thus function to shield the laminate region, which at this stage is very delicate and presumably is appetizing to predators. At an earlier stage of stem development the stipules also function to protect the next frond developed (Bierhorst, 1971) whilst later, after unfurling of the crozier, they more or less tightly clasp the swollen basal region of the rachis (Fig. 5B; Shove, 1900; Brebner, 1902; Ogura, 1972). They persist permanently on the stem after detachment of the fronds. We have found that the cells of the stipules contain abundant starch grains. Stipules are therefore recognised here as a form of trophopod, sensu Wagner & Johnson (1983).

It is widely accepted that all extant Marattiales possess stipules, though for many described species they have not been recorded by the authors and have rarely been collected. Since their form is constant for a plant but varies from plant to plant, particularly in the detailed characters of the margin, they may be useful for discriminating species (Holttum, 1978).

The term 'stipule' has also been applied to the sheathing structure formed from the expanded basal region of the 'aerial complex' (sensu Bierhorst, 1971) in Ophioglossales. Differences from Marattiales are as follows: (*a*) In Ophioglossales the so-called 'stipules' are thin, non-vascularised and scarious, whilst in Marattiales they are vascularised and relatively massive. (*b*) In Ophioglossales they do not store starch (determined from thin sections stained with iodine in potassium iodide solution). (*c*) The 'stipules' of Ophioglossales, as we understand them, are at least initially in their development a single sheath. This completely encloses the next aerial complex developed, to form a 'bud' (Bierhorst, 1971). Subsequent growth of the complex ruptures the sheath and this often gives it the appearance of two stipules (Bierhorst, 1971; cf. Sporne, 1975). Further work on live plants is needed, however, to clarify these observations for each of the three genera. (*d*) Adventitious buds and lenticels often occur on the stipules of Marattiales but never on the sheaths of Ophioglossales.

Of these comparisons, (*c*) in particular suggests that the sheath of Ophioglossales is not homologous with the stipules of Marattiales, except in the functional sense of an organ providing protection during early frond development. Apomorphous features (not shown in Fig. 23) of extant marattialean stipules compared to the sheaths of Ophioglossales are (*a*) their clear occurrence in pairs; (*b*) their function (besides protection) for photosynthesis and for storage of starch; (*c*) their relatively massive substance; (*d*) possession (in some species) of lenticels; (*e*) their ability to produce adventitious buds; and (*f*) their vascularisation.

Although radically different in form from ordinary pinnae, it is generally held that the stipules of extant Marattiales represent reduced pinnae. Their association with the basal pulvinus of the rachis, and the association generally of pinnae and pinnules with pulvini (characters 6, 26–28), provides some indirect evidence for this belief. There is also some indirect support from certain fossils referred to the form genus *Aphlebia* Presl (Scott, 1920; Kidston, 1924; Crookall, 1976). These range in form from some species rather similar to the stipules of extant Marattiales to others that are pinnate in construction and therefore more clearly represent reduced pinnae, such as *A. spinosa* Lesquereux, *A. acanthoides* Zeiller and *A. crispa* (Gutbier) Presl (see e.g. Crookall, 1976).

Some species of *Aphlebia* are known to occur in field association with *Scolecopteris*, and also with *Pecopteris* Brongniart and *Asterotheca* Presl (*Asterotheca* and some species of *Pecopteris* are attributed to Psaroniaceae). However, the only forms known in actual attachment to pecopterid fronds are securely attributed to other families, such as the remarkable aphlebiae which occur at the bases of the pinnae in the fronds of *Senftenbergia plumosa* (Artis) Stur, figured by Kidston, 1924, Pl. XCIII, figs 2–4. These (for *S. plumosa*) resemble *Aphlebia spinosa* and therefore this very deeply dissected form of aphlebia may be dismissed in connection with Marattiales. *Aphlebia acanthoides* Zeiller is considered by Crookall (1976) on evidence of field association to have been 'almost certainly borne' by fronds of *Asterotheca daubreei* Zeiller. It is essentially bipinnate and to that extent pinna-like, but the divisions are merely cut into lobes. Such a form may be considered intermediate between a pecopterid pinna and the form of stipule seen in extant Marattiales. *Aphlebia crispa* (Gutbier) Presl (Gutbier, 1835: 13, pl. 1, fig. 11 and ? pl. 6, fig. 18; see also Crookall, 1976), although two to three times pinnate, has a broader axis and has lobes that are rather more flabelliform and decurrent than in *A. acanthoides*, the lobes having lacerate margins. Each primary lobe approaches (more closely than in *A. acanthoides*) the most deeply divided form of stipule found in extant Marattiales, though considerably more deeply incised in the fossils than in extant material. *Aphlebia membranacea* Lesquereux (see Crookall, 1976) has a broad main axis, is only once-pinnate and the divisions are distinctly flabelliform lobes, irregularly divided and with a fimbriate margin. Therefore in many respects it resembles a stipule of living Marattiales. *Aphlebia flabellata* Sternberg is still more flabelliform, without a clear 'midrib' (Hirmer, 1927) and also has a partly fimbriate margin. To this extent we consider *A. flabellata*, together with some other species such as *A. linearis* (Gutbier) Presl, may show the nearest approach to stipules of extant Marattiales. An *Aphlebia* species (cf. *A. crispa*) with lobes somewhat similar to those of some extant marattialean stipules is illustrated for comparison with them in Fig. 6.

Although a sequence of forms of *Aphlebia* could be proposed by which pecopterid pinnae may have become progressively reduced, and although there is some evidence from field association that such forms were borne by psaroniacean fronds, there is no direct evidence for either. In contrast there is direct evidence that several different groups of ferns and fern-allies bore aphlebiae of varied form. Therefore any proposed evolutionary sequence based on detached forms alone must be viewed with extreme caution. Only two generalisations are at all clear from the fossil evidence: firstly, that aphlebiae generally functioned in the same way as the stipules of extant Marattiales to protect fronds and/or individual pinnae at the crozier stage and during unfurling of the frond. They were located at the sites where pulvini generally occur today in marattialean fronds (excluding mid-stipe pulvini). Secondly, it seems that possession of stipules and aphlebiae is a plesiomorphous feature of ferns and their allies. We speculate that they served to protect megaphyllous fronds at their most tender (and palatable) stage of ontogenetic development, at a stage in their evolutionary development before the plants had evolved the battery of chemical defences that today deters many animals from eating their young fronds. Such a supposition is testable to an extent from the comparative biochemistry of extant taxa. Marattiales and Ophioglossales at crozier stage would be expected to have fewer such chemical deterrents, or at any rate less sophisticated ones, than Filicales.

More particularly we cannot conclude that Psaroniaceae definitely had stipules. The evidence that they had aphlebiae is merely based on general field association and is at best of structures that are only approximately stipular in form. Stipules (or aphlebiae) were lacking from the young *Psaronius* sporophytes described by Stidd & Phillips (1968), one of which had five leaf traces and some attached petiole bases. (In extant Marattiales, stipules do not occur on the first frond of the young sporophyte but are soon developed on later ones, the second in *Christensenia*, the third in *Marattia* and *Angiopteris*, though sometimes not until the fourth in *Danaea* (Farmer, 1892; Campbell, 1908, 1911)). Older stems of *Psaronius* are difficult to evaluate, since only the apical region of the stem surface is at all directly comparable with that of extant Marattiales. So far as we are aware, these apical regions of *Psaronius* lack persistent stipules. There is equally no evidence of stipules in the more proximal regions, which is to be expected in view of their dense development of external root mantle.

In conclusion, the overall evidence as to whether Psaroniaceae had stipules (or aphlebiae) is not clear. Until such organs may be found in attachment or very convincingly associated, we suggest *Psaronius* lacked them. Even if it had them they were clearly not persistent.

6. *Pulvini* (Fig. 2). These are regions of the frond axis that in live plants are more or less pale in colour and swollen but in herbarium specimens are usually dark and shrunken. They occur above the stipules at the base of the stipe, sometimes elsewhere on the stipe but at some distance proximal to the lamina and at the junctions of pinnae or pinnules with the frond axes. Unlike other parts of the stipe and frond axes they have a hypodermal layer of collenchyma rather than sclerenchyma, as illustrated by Chang (1975), and a ring of mucilage canals may occur between the band of collenchyma and the epidermis (Sachs, 1882; Gwynne-Vaughan, 1905; Brebner, 1902; Chang, 1975).

Takhtadzhyan (1956) and Chang (1975) consider the pulvini function to orientate the frond lamina in relation to sunlight. According to Chang, Hayata's (1928) discussion of *Archangiopteris* 'pointed out the fleshy nodose swellings on the middle of the stipes as resulting from ecological adaption, helping the plant to drop its leaves at this point under dry conditions'. Holttum (1978) comments for *Angiopteris*: 'In dry periods of weather . . . the loss of water from cells in the pulvini causes the whole frond to droop, and also each separate pinna'. The pulvini can also act as points of detachment of senescent pinnules as shown by Croft's field observations (pers. comm. 1983) and our own observations of Marattiales grown at K. Holttum (1978) writes that the size of pulvini is a distinctive specific character in the living plant.

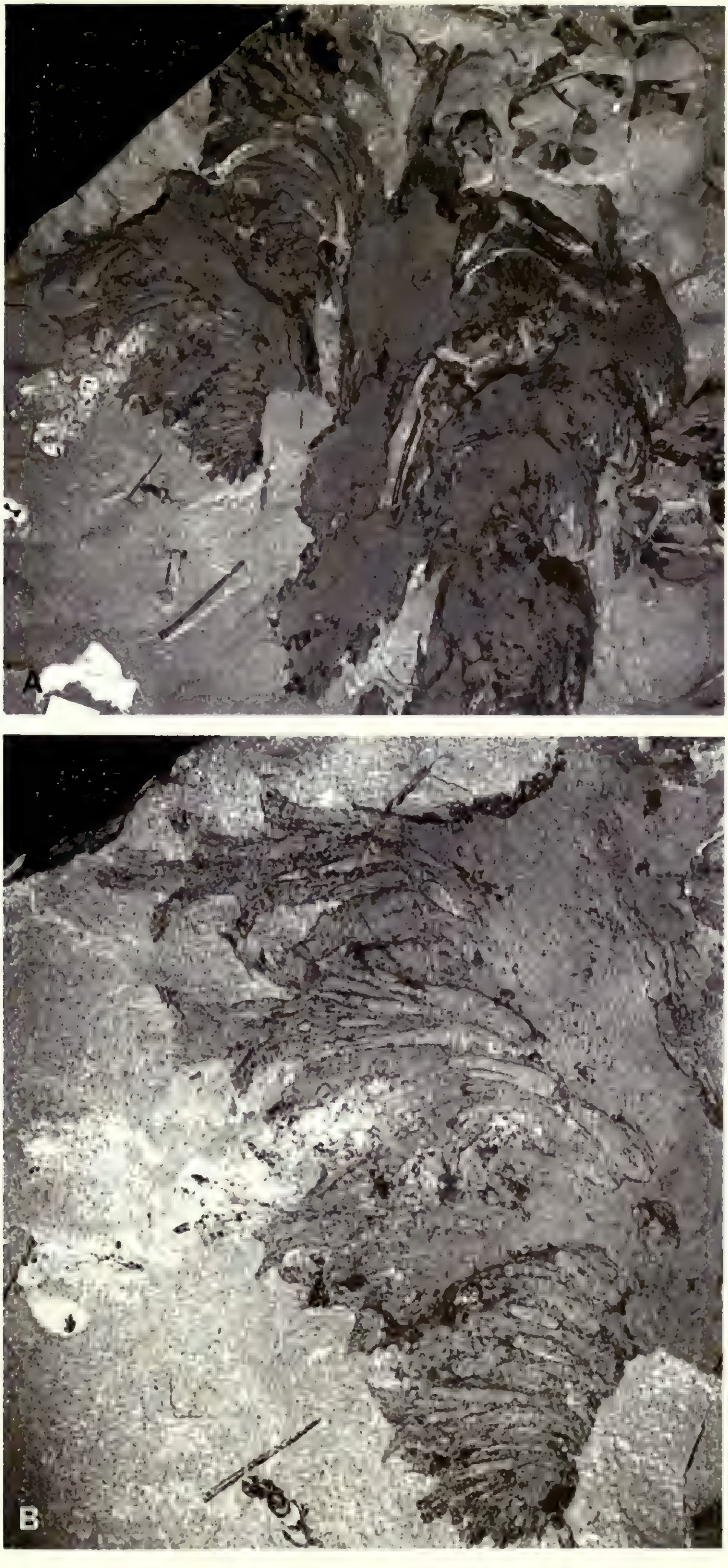
7–10. *Mucilage canals* (Fig. 4A). The lysigenous origin and development of these in extant Marattiales is documented by West (1915). Mucilage cells are known to occur in some other distantly related filicopsids (especially Cyatheaceae), but canals are rarely formed. Since they are absent from Ophioglossales the occurrence of mucilage canals of the kind seen in Marattiales is considered to be apomorphous for the order.

Mucilage canals have been recorded from some *Psaronius* stems (Morgan, 1959; Stidd, 1971; DiMichele & Phillips, 1977) but not others (Rothwell & Blickle, 1982). They have not been reported from the roots of *Psaronius*. Millay (1979: 39, pl. 15, fig. 108) however, shows such canals for pinnules of *Scolecopteris* and Stidd's (1971) 'lacunae' indicate their occurrence in the axial components of the *Scolecopteris* frond. In our root sections of some species of *Archangiopteris* not included in the cladogram, mucilage canals were not visible: *A. tamdaoensis* (*Hayata* s.n., Vietnam, 4 August 1917 (TI)), *A. 'variabilis'* Ching (ms name) (*Wu Ligong* 4196, SE. Yunnan (PE)), *A. henryi* var. *somai* (collector not known, Taiwan (PE)), *A. subintegra* Hayata (collector not known, Tonkin, Vietnam, September 1932 (P)) and *A. 'brevipetiolata'* Ching (ms name) (*Feng Guo-Mei* 5078, SE. Yunnan (PE)).

Campbell (1914*b*) did not report mucilage canals in the roots of young *Macroglossum* plants, though we have seen them in the roots of a mature plant. Mucilage canals running parallel with and below the veins under the sori were considered by Campbell (1914*a, b*) to be unique to *Macroglossum*. However, we have found them also in our sections of five other of the terminal taxa shown in Fig. 23 and in *Angiopteris polytheca* C. Chr. & Tard. (*Poilane* 2370, Laos (BM)).

11. *Sclerenchyma in the stem cortex*. Holle (1876) reported a layer of sclerenchyma in the outer cortex of the stem of a specimen of *Danaea trifoliata* Reichb. Later authors (Kuhn, 1890; Brebner, 1902; Campbell, 1911) did not see this feature in their studies of *Danaea*, and since Holle had not mentioned stipules on his specimen, it was assumed that it was not a *Danaea*. However, this layer of sclerenchyma definitely does occur in *Danaea*. We have found it both in creeping and erect rhizomes of specimens of *D. elliptica* Smith (*C. Whitefoord* 1215, Belize (BM)), *D. fendleri* L. Underw. (*N. Y. Sandwith* 1786, Tobago (BM)), and *D. moritziana* C. Presl (*A. H. G. Alston* 8539, Colombia (BM)). In these the layer is one to three cells thick. In a specimen of arborescent habit this layer is well-developed and may be up to eight or nine cells thick. (*Persaud* 76, Guyana (K, NY, UG): *D.* sp. A of this paper, illustrated in Figs 2, 3, and 4A, B). Sclerenchyma in the stem cortex has not, however, been seen in other extant Marattiales. In

Fig. 6 A fossil *Aphlebia*, cf. *A. crispa* (Gutbier) Presl. Upper Carboniferous, locality unknown, V.2865. **A**, Showing the broad midrib with several pinnae. × 1. **B**, Close-up of bottom pinna at left in A to show lacerate margin. × 2·5. Compare with the stipule margins in Fig. 5.


A
B

Psaronius, the peripheral sclerenchyma of the cortex may occur either as longitudinal bands, or, as in extant *Danaea*, as a cylinder, and is absent from some specimens.

Sclerenchymatous tissue is absent from the stems of Ophioglossales but occurs in those of many other pteridophytes, e.g. Polypodiaceae s.s., Cyatheaceae, Hymenophyllaceae. We consider these to be homoplasious occurrences with Marattiales. Unlike the Polypodiaceae and Hymenophyllaceae the development of such tissue in Marattiales may be correlated with an arborescent habit, at any rate ancestrally.

12–13. *Root sclerenchyma*. We have examined the roots of five *Angiopteris* species, five of *Marattia*, three of *Archangiopteris* and *Macroglossum smithii*: *Angiopteris canaliculata* Holttum (*R. E. Holttum* s.n., New Guinea [BM + pteridophyte spirit collection W. 393; K hort. 578–63.57807]), *A. elliptica, A. evecta, A. boivinii* Hieron. (*M. J. Whitehead* 56, Seychelles [BM pteridophyte spirit collection S.280; K hort. 301–73.04156]), *Marattia laevis, M. douglassii* (C. Presl) Baker (*A. C. Jermy* 8345, Hawaiian Islands [BM pteridophyte spirit collection S. 276; K hort. 272–70.02662]), *M. novoguineensis* Rosenstock (*Sands, Pattison & Wood* SPWX 1429, Papua New Guinea [BM pteridophyte spirit collection S.282; K hort. 330–75.03192] and *J. R. Woodhams* s.n., New Guinea [BM pteridophyte spirit collection S.275; K hort. 003–74.00163]), *M. laxa* Kunze (*R. I. Beyer* RIB.108, Mexico [BM pteridophyte spirit collection W.394; K hort. 175–78.01730]), *M. rolandi-principis, Archangiopteris caudata* Ching, *A. hokouensis* Ching, and *A. tamdaoensis* (*Hayata* s.n., Tamdao, Vietnam, 4 August 1917 [TI]). Not one of these shows sclerenchymatous tissue in either pith or cortex of the root. *Protomarattia tonkinensis* Hayata has hypodermal collenchyma which contains some sclerified cells.

In contrast, all the species of *Danaea* examined had sclerenchymatous tissue in the root pith and also as a hypodermal layer in the root cortex, as shown in Table 2. These two zones of sclerified tissue are illustrated in Fig. 4A, in a root passing vertically through the stem cortex prior to its emergence, as in the apex of *Psaronius*. Unlike the occurrence of such tissue in the stems, there is no obvious adaptive explanation for this occurrence of sclerenchyma in marattialean roots, excepting possibly that greater stress on roots (as prop-roots) of forms with arborescent stems, coupled with evolutionary conservatism, might be considered to indicate that *Danaea* was primitively arborescent.

Root sclerenchyma has not been reported from Ophioglossales. By outgroup comparison we therefore consider it to be the derived character state.

15. *Root hairs*. Brebner (1896) reported multicellular root hairs in a young sporophyte of *Danaea simplicifolia* Rudge and comments that they had not been reported for *Angiopteris* or *Marattia*. Campbell (1911) interpreted them as septate hairs and recorded them for *Danaea elliptica, D. jamaicensis* L. Underw., and *Christensenia*. West (1917*a*) illustrates the same feature in a transverse section of the root of *Danaea alata* Smith.

Since we have seen nuclei in some of these hairs (Fig. 4C, D) we accept Brebner's interpretation of them as multicellular. They appear always to occur mixed with ordinary unicellular hairs and are easy to overlook. We have seen them in *Angiopteris canaliculata* (*R. E. Holttum* s.n., New Guinea [BM pteridophyte spirit collection W.393, K hort. 578–63.57807]), *A. evecta, A. boivinii* (*M. J. Whitehead* 56, Seychelles [BM pteridophyte spirit collection S. 280, K hort. 301–73.04156]), *Macroglossum smithii, Marattia novoguineensis* (*Sands, Pattison & Wood* SPWX 1429, Papua New Guinea [BM pteridophyte spirit collection S.282, K hort. 330–75.03192]) and *J. R. Woodhams* s.n., New Guinea [BM pteridophyte spirit collections S. 275, K hort. 003–74.00163]), *M. laevis* (*A. C. Jermy* 8345, Hawaiian Islands [BM pteridophyte spirit collection S.276, K hort. 272–70.02662]), *M. laxa* (*R. I. Beyer* RIB.108, Mexico [BM pteridophyte spirit collection W.394, K hort. 175–78.01730]), *Christensenia aesculifolia*, and *Danaea* sp. A. We therefore predict that they are a universal character of extant Marattiales. Since root hairs in pteridophytes are typically unicellular, this character is also considered apomorphous (Bary, 1884; Bierhorst, 1971; Ogura, 1972). Root hairs have not been recorded from *Psaronius*, nor from Ophioglossales, which have mycorrhizal roots (Bierhorst, 1971). We have therefore adopted the polarity absence = plesiomorphous and presence = apomorphous.

17–19. *Habit and symmetry of adult stem.* West (1917*b*) and Chang (1975) interpreted *Danaea alata* and *Archangiopteris henryi* as having dorsiventral rhizomes, but we consider only *Christensenia* to be truly dorsiventral. *Danaea, Archangiopteris* and *Protomarattia* all show fronds emerging both from the lateral and ventral surfaces of the rhizome as well as from the dorsal surface, as opposed to solely from the dorsal surface in *Christensenia*. Amongst Ophioglossales, *Helminthostachys* has a dorsiventral rhizome. Our choice of polarity for this character is therefore based on 'pteridophytes' as a whole, for which the dorsiventral state is generally considered apomorphous.

Observation of populations in the field is needed to clarify the extent of the distinction drawn between erect rootstocks vs creeping rhizomes, and which we have had to base largely on limited collections of dried specimens.

Figures 2 and 3 illustrate the elongate erect stem of *Danaea* sp. A, which in some respects shows a remarkable resemblance to the fossil stem *Psaronius*.

20–23. *Pinnation of mature fronds.* The 'mature' frond is considered here to be the stage of development that bears sporangia. This is usually also the most mature stage in terms of degree of pinnation. Rare instances are known, however, where earlier stages of pinnation may also bear sporangia, for example simple-leaved herbarium specimens (BM) of *Christensenia* and once-pinnate fronds of *Angiopteris lygodifolia* Rosenstock (Asama, 1960). This causes problems in describing the degree of pinnation of the mature developmental stage of *A. annamensis* C. Chr. & Tard., because it is known from only a few specimens which show equally both once-pinnate and twice-pinnate mature fronds. The developmental sequence of frond forms in extant Marattiales is summarised in Fig. 7.

Although a binary treatment is used for pinnate vs palmate frond development, the palmate frond of *Christensenia* is probably the result of evolutionary condensation of a complex pinnate frond form. There is, however, no positive evidence for this from the vasculature of mature fronds. There is a comparable range of 'frond' dissection within the aerial complexes of Ophioglossales. *Botrychium* is pinnatified to 3-pinnate, *Helminthostachys* approximately palmate, whilst *Ophioglossum* is simple or dichotomously forked. We consider (by reference to 'trimerophytes') that the highly dissected frond form of some species of *Botrychium* is the most generalised state in Ophioglossales, and therefore also in Marattiales.

24. *Transverse ridges on stipe of mature fronds.* An apparent homologue of this feature occurs in *Marattia brooksii* Copel. Neither it nor *Angiopteris annamensis* have been examined anatomically and the ridges may merely represent some kind of pathological growth response.

This character does not occur in Ophioglossales. By comparison within Marattiales its occurrence is considered to be the derived state and its absence as generalised.

25. *Soft spines on the veins of the pinnules.* These occur in *Marattia laevis*, mainly on the upper surface, but in some specimens also on the lower. Measurements of 35 spines from several herbarium specimens gave their length as (0·22–)0·56(–1·3) mm, and their width just above the decurrent base as (0·04–)0·12(–0·2) mm. No homologous feature has been reported from fossil foliage, but appendages of similar size and shape have been described from *Psaronius* (termed 'scales') by Stidd & Phillips (1968).

This character does not occur in Ophioglossales. By comparison within Marattiales its occurrence is considered to be the derived state and its absence as generalised.

26–28. *Pulvini on the frond stipe* (Fig. 2). Hayata (1928) transferred *Archangiopteris somai* Hayata, *A. subintegra* and *A. tamdaoensis* to his now obsolete genus *Protangiopteris* partly because he considered a pulvinus was lacking from the mid-region of their stipes. However, he had earlier (1919) recorded a pulvinus in this position for the type specimen of *A. tamdaoensis* (TI). *Archangiopteris henryi* is figured and described by Christ & Giesenhagen (1899) as lacking this pulvinus in the mid-region of the stipe, but Hayata did not transfer this species to *Protangiopteris*. In fact all specimens of *Archangiopteris* and *Protomarattia* do show a pulvinus

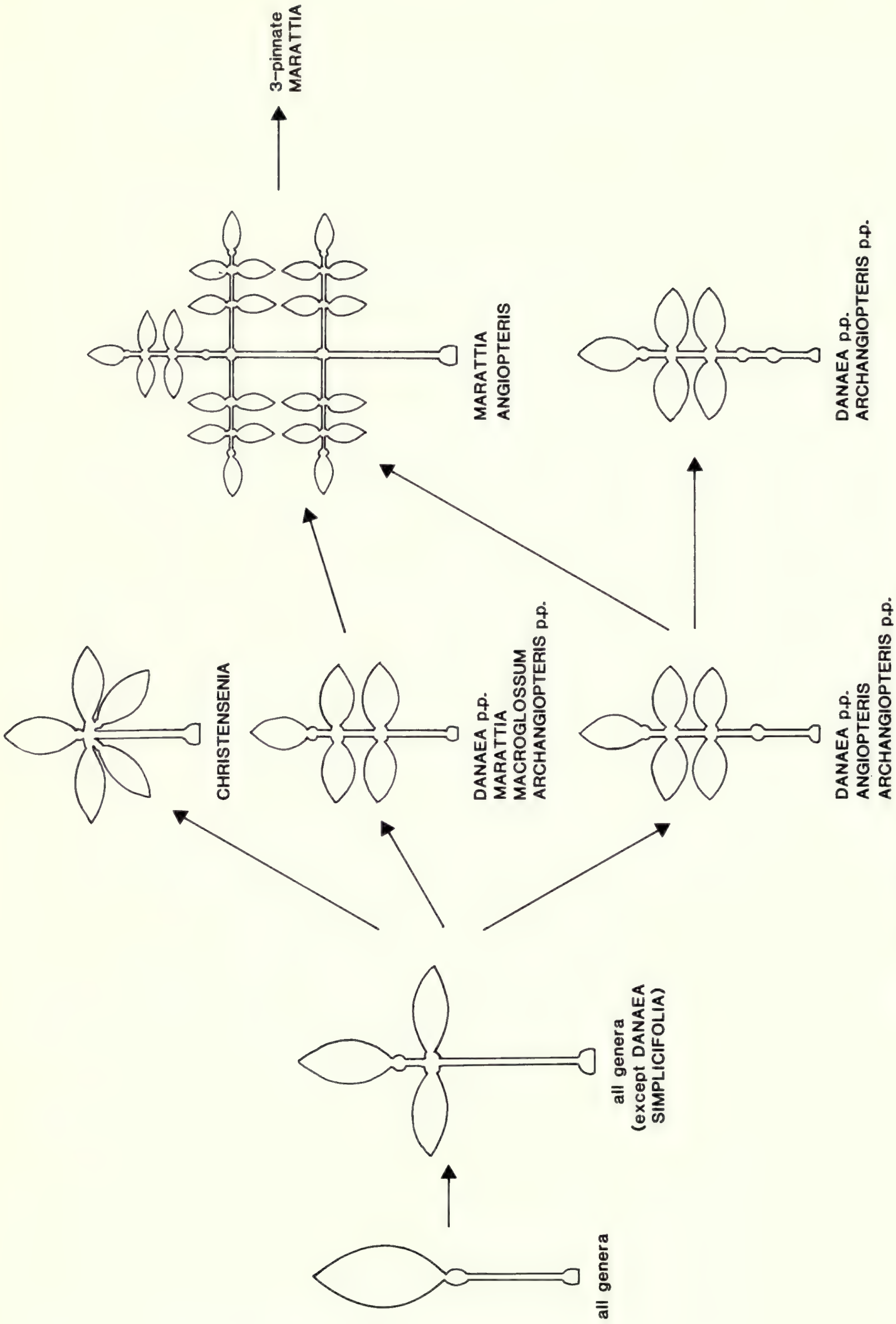

all genera
all genera (except DANAEA SIMPLICIFOLIA)
CHRISTENSENIA
DANAEA p.p. MARATTIA MACROGLOSSUM ARCHANGIOPTERIS p.p.
DANAEA p.p. ANGIOPTERIS ARCHANGIOPTERIS p.p.
MARATTIA ANGIOPTERIS
DANAEA p.p. ARCHANGIOPTERIS p.p.
3–pinnate MARATTIA

Fig. 7 Diagram of developmental sequence of frond forms of extant Marattiales.

in the mid-region of the stipe of fertile fronds. It is very clear in the type specimen of *A. henryi* (P), and Gwynne-Vaughan (1905) reported it for the material of *A. henryi* collected by Henry and preserved in spirit. (Gwynne-Vaughan's preparations are in the Department of Botany, University of Glasgow.)

Ching (1958*b*) and Chang (1975) also consider a pulvinus in the mid-region of the stipe to occur in all individuals of *Archangiopteris*. Chang (1975) suggested that the occurrence of this character in all *Archangiopteris* fronds but only in the juvenile, once-pinnate fronds of *Angiopteris* (confirmed by Hayata's and our own observations) indicates neotenous descent of *Archangiopteris* from *Angiopteris*. *Angiopteris annamensis* is the only species of *Angiopteris* normally having fertile fronds that may be either once or twice pinnate. It might provide such a link between these two genera.

With so few species of Marattiales in cultivation there is little information available on this character for juvenile fronds. However, plants produced from adventitious buds on the stipules apparently pass through the same ontogenetic stages as plants raised from spores and therefore this evidence has been used provisionally instead. Of the live Marattiales observed in this way at K, none of the *Marattia, Christensenia*, or *Macroglossum* plants produced juvenile fronds with a pulvinus. However, all the *Angiopteris* juvenile fronds were found to have a pulvinus in the middle region of the stipe. Fig. 7 illustrates the developmental sequence of frond forms in extant Marattiales, with the positions of the pulvini indicated.

Vareschi (1969) comments that the number of pulvini developed on the stipe is very variable in any one species of *Danaea*. However this does not seem to hold for all species of the genus. Vareschi possibly confused pulvini on the stipe with pulvini left on the rachis after detachment of pinnae and it is also possible that he treated several species as one. In this study the pulvinus on the stipe of *D. simplicifolia* is interpreted as the pulvinus basal to the lamina rather than the one in the middle region of the stipe.

Pulvini do not occur in Ophioglossales and Psaroniaceae. By outgroup comparison their occurrence in extant Marattiales is therefore considered the derived character state.

29. *Microscopic projections from exterior of walls of spongy mesophyll cells.* These extraordinary intercellular rods illustrated in Figs 8 and 9 were first reported by De Vriese in De Vriese & Harting (1853) who saw them through the stomatal openings of *Kaulfussia assamica* De Vriese (now synonymised with *Christensenia aesculifolia*). Luerssen (1875*b*) found them in the petioles, stems and roots of *Angiopteris evecta* and of *Marattia cicutaefolia* Kaulf. but was uncertain whether the structures seen in *Danaea elliptica* were truly such rods or fungal mycelia. He thought their composition was 'cuticular cellulose' and also reported their occurrence in members of Cyatheaceae, Polypodiaceae s.l., Osmundaceae and Ophioglossaceae. Bary (1884) considered them to be local thickenings of the cell wall membranes, whilst Gardiner (1885) thought that in '*Aspidium filix-mas, Blechnum brasiliense* and other ferns' they were composed mainly of mucilage. Schenk (1886) concludes that they are neither pure cellulose nor wax and comments that their biological significance is completely enigmatic. Campbell (1911) claims they are 'mainly composed of calcium pectinate'.

Dr J. M. Pettitt has examined these structures cytochemically and with TEM. He found that alcian blue at pH 2·5, dialysed iron and the periodic acid – Schiff (PAS) method were all positive (the first two strongly so, PAS faintly positive), indicating the presence of polysaccharides. Staining with coomassie blue and oil red O were negative, suggesting that the projections do not contain protein or lipid. His electron micrograph (Fig. 9) shows that these structures are composed of microfibrils orientated the same way as those of the mesophyll cell wall, but that they seem to have been formed by successive layers of material laid down after the formation of the cell wall. We have also seen these projections in *Helminthostachys* (Ophioglossales) but not in other members of this group. We therefore regard their occurrence as a derived character state within both Ophioglossales and Marattiales.

30. *Guard cells and lenticels.* Campbell (1911) writes 'The stomata of *Kaulfussia* (= *Christensenia*) have long been known for their great size and the fact that they form permanently open

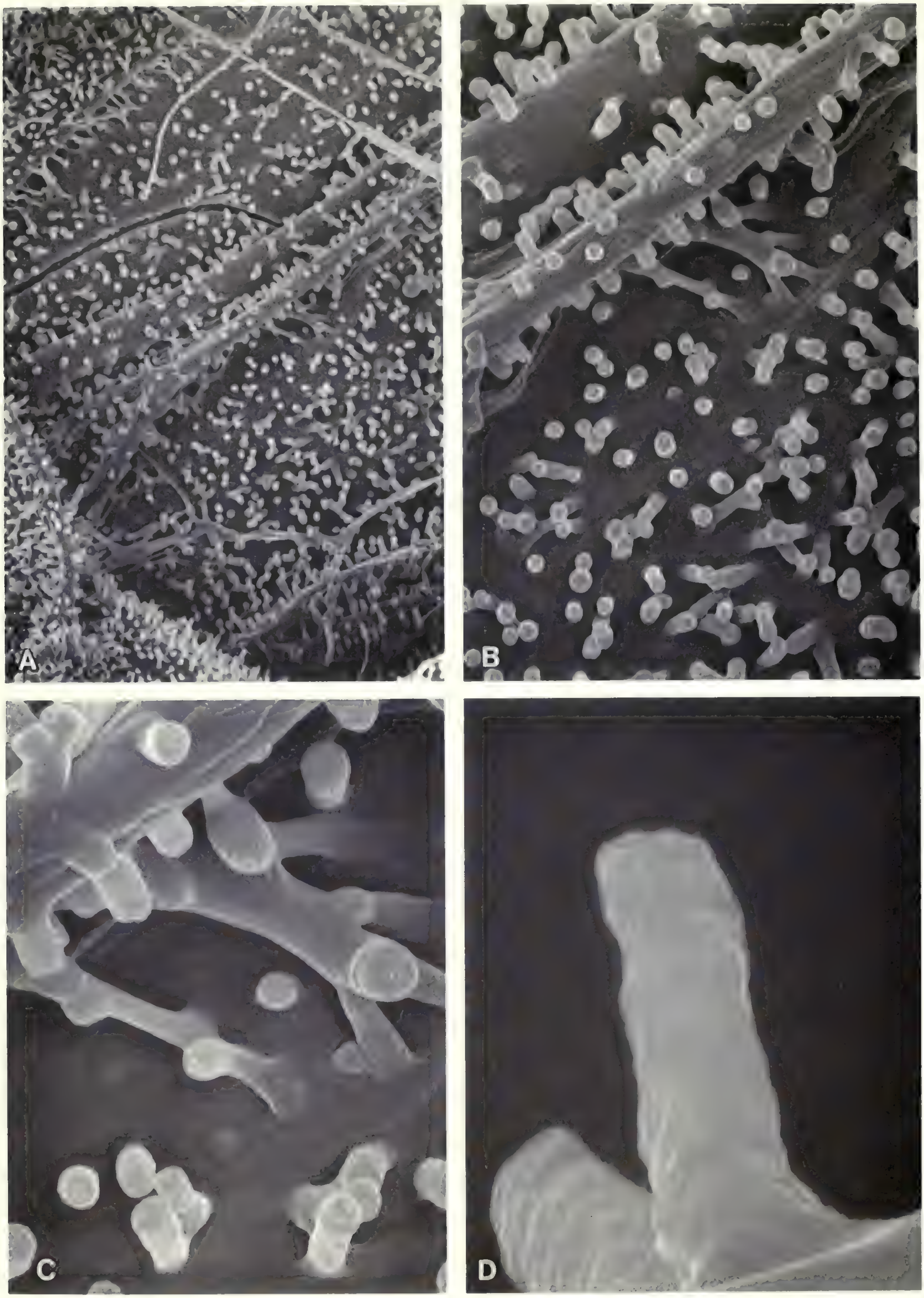


Fig. 8 *Christensenia aesculifolia* (Blume) Maxon, *Griffith* s.n., Assam, (BM): projections from exterior of walls of mesophyll cells (character 29). SEM photographs, Hitachi S 800, A × 1500, B × 4000, C × 10000, D, × 50000.

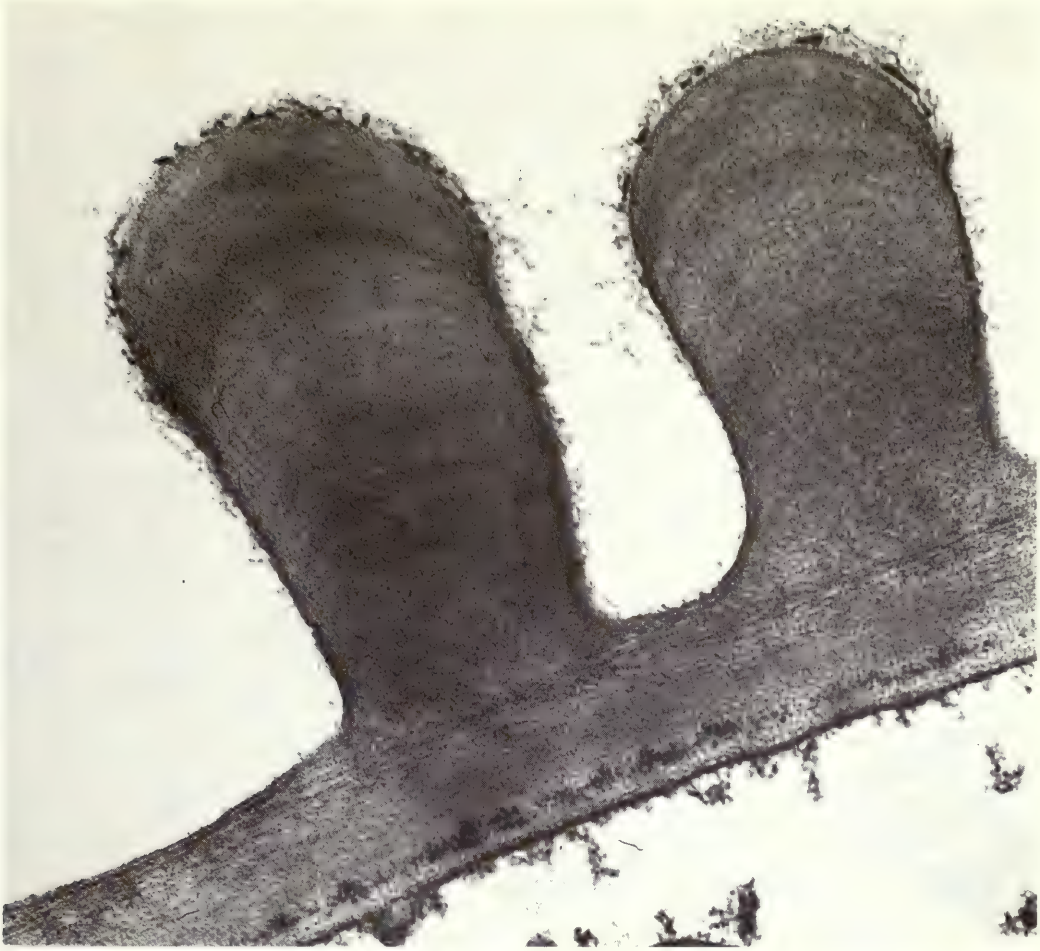


Fig. 9 *Macroglossum smithii* (Racib.) Campbell, *A. C. Jermy* 14223, Sarawak (Kew hort. ref. 279–78.03064): projections from exterior of walls of mesophyll cells (character 29). TEM (Hitachi HS 9). × 40000. Photograph by J. M. Pettitt.

pores, a peculiarity already developed in the cotyledon'. They are the largest of any vascular plant. Although De Vriese in De Vriese & Harting (1853) does not actually comment that *Christensenia* stomata are permanently open, his observations indicate that he was the first to observe this (see discussion of character 29). SEM photographs of herbarium material show open stomata in *Christensenia* and closed ones in other extant genera. Scott & Holden (1933) illustrate the stomata of *Scolecopteris oliveri* Scott with preserved guard cells.

Holttum (1978) comments incisively on the different pattern of lenticel distribution in *Angiopteris* compared to members of the Filicales. In this genus, and also in large plants of *Marattia* and *Danaea*, lenticels are found scattered all over the stipe and rachis (Fig. 5). In contrast in large plants of, for example, Cyatheaceae, Dicksoniaceae, Dennstaedtiaceae, and Thelypteridaceae, the aerating tissue occurs in two lateral bands on the frond axes. We have found neither stomata nor lenticels in the epidermis of the stipe of *Christensenia*.

31–33. *Subsidiary cells of the stomata.* (Fig. 10B, D, F). Although Van Cotthem (1970) describes the stomata of Ophioglossaceae and a few genera of Polypodiaceae as cyclocytic, his illustrations appear to us to show anomocytic to only weakly cyclocytic stomata. Strongly cycloctyic stomata appear to be unique to Marattiales amongst extant filicopsids.

The ontogeny of the guard cells and subsidiary cells has been studied in only four species of

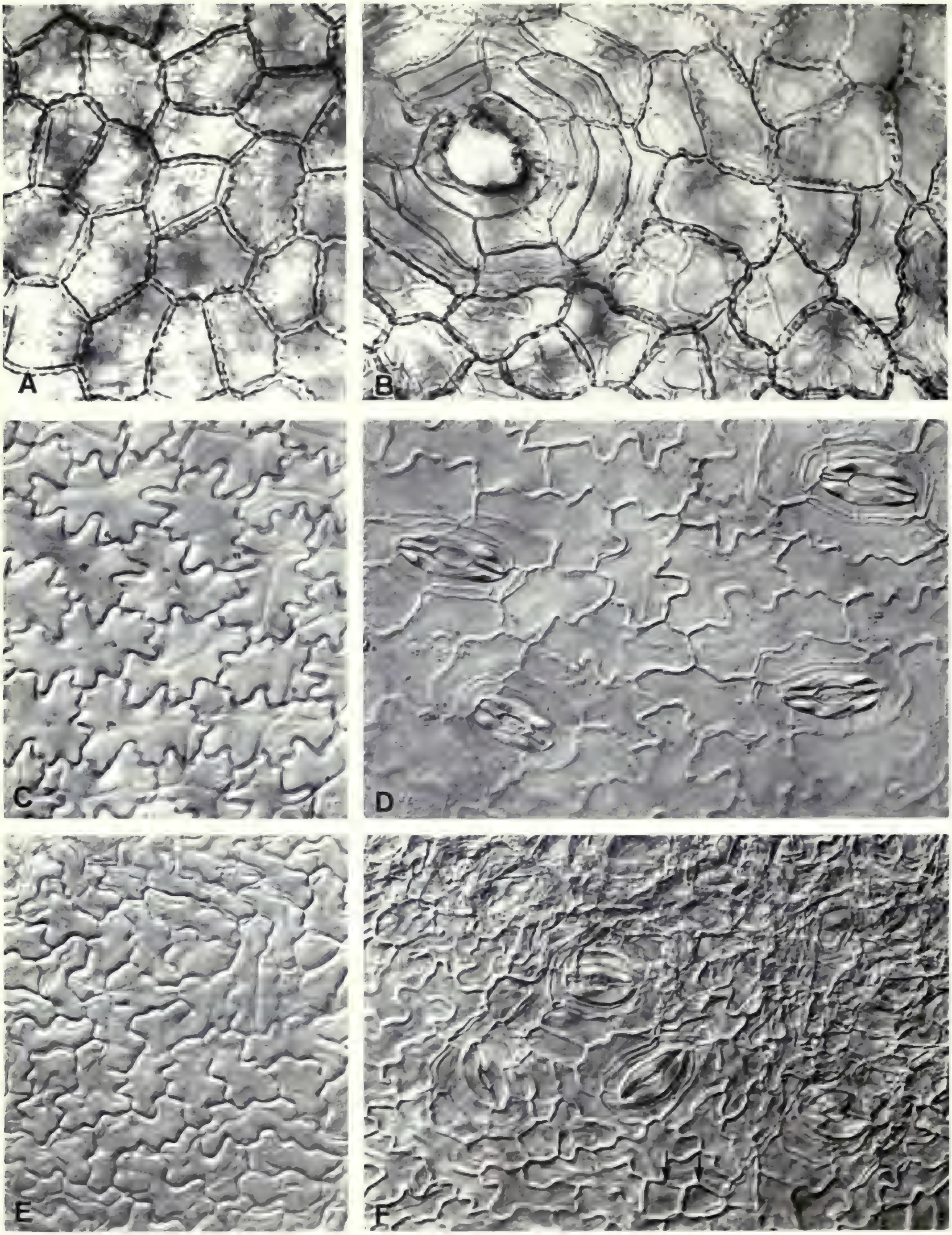


Fig. 10 Epidermal characters (characters 30–36). **A, B**, *Christensenia aesculifolia* (Blume) Maxon, *Zollinger* 1902, Java (BM). A, Upper epidermis of frond and B, lower epidermis. × 200. **C**, **D**, *Danaea elliptica* Smith, *G. Aldridge* 1834, Trinidad (BM). C, Upper epidermis of frond and D, lower epidermis. × 200. **E**, **F**, *Marattia fraxinea* Smith, *H. Humbert* 8417, Zaire (BM). E, Upper epidermis of frond and F, lower epidermis; idioblasts arrowed. × 200. C–F, Interference contrast, photographs by C. H. Shute.

Angiopteris (Kondo, 1962; Pant and Khare, 1969), with some apparent conflict in the developmental stages seen. Our preparations indicate that the difference in the arrangement of the mature subsidiary cells in *Danaea* compared to *Marattia, Angiopteris, Macroglossum, Archangiopteris,* and *Protomarattia* is slight (character 32).

34. *Stomatal dimensions* (Table 1). Different cytological races are known to occur in Marattiales (Braithwaite, 1977; Walker, 1979), including *Christensenia*. Stomatal dimensions of two cytological voucher specimens (*T. G. Walker* T 13319, n = 40 [BM]; *A. F. Braithwaite* R.S.S. 4220, n = 80 [K]) were compared with those of five other specimens of *Christensenia*. The results did not indicate that the level of ploidy is expressed in terms of stomatal dimensions.

35. *Walls of epidermal cells.* Van Cotthem (1970) surveyed the epidermal characters of *Pteridium aquilinum* (L.) Kuhn from Europe, the Americas, Africa, and Asia. His results showed that most characters of the epidermal cells vary greatly, for example cell shape and dimensions and sinuosity of their anticlinal walls. Such variation is also seen in Marattiales and Ophioglossales. However, the kind of sinuosity seen in the anticlinal walls of the ordinary epidermal cells of *Christensenia* (Fig. 10) is consistently different from that shown by all the other extant genera of these two groups and is therefore regarded as an apomorphous character state.

Details of the walls of the epidermal cells of *Scolecopteris oliveri* are not obtainable from the slides of Scott & Holden (1933).

36. *Idioblasts.* These are approximately isodiametric cells with more or less granular contents. They frequently occur in pairs amongst the commoner, larger, and more oblong ordinary cells of the lower epidermis of most extant species of Marattiales (Fig. 10F) and also occur in the stem parenchyma. Christ & Giesenhagen (1899) termed them 'kieselzelle' and recorded their presence in *Archangiopteris* and *Angiopteris* but absence from *Danaea*. This term has been translated as 'silica-cell' and is so used by Pant & Khare (1969), Van Cotthem (1970), and Ogura (1972). There is, however, no evidence to suggest the cells contain silica. Their contents are dissolved in NaOCl solution as used in this study and by Van Cotthem (see his figs 13 & 18, where the characteristic cells are shown without contents) and silica is not soluble in aqueous NaOCl. Translation as 'stone-cell' is equally inadvisable as these cells bear no resemblance to sclereids.

The contents of these cells have also been variously considered to consist of gypsum, calcium oxalate and 'Kalilauge' (potassium hydroxide) (Hansen, 1888; Rothert, 1887; Christ & Giesenhagen, 1899).

Idioblasts are not known to occur in Ophioglossales.

37–39. *Lamina margin and 'fibre' bundles.* The Marattiales used for the cladogram all have toothed or lobed lamina margins. In some species, however, the division of the margin is barely

Table 1 Summary of stomatal dimensions of extant genera of Marattiales.

	Angiopteris *Macroglossum* *Archangiopteris* *Marattia*	*Christensenia*	*Danaea*
Length of stomata μm (stoma + guard cells)			
Van Cotthem (1970: 97)	35–65	125–145	65–80
Pant & Khare (1969) (*Angiopteris evecta*)	47–73		
this study	36–76	65–270	56–92
Breadth of stomata μm (stoma + guard cells)			
Van Cotthem (1970: 97)	20–35	80–110	20–35
Pant & Khare (1969) (*Angiopteris evecta*)	13–17		
this study	28–44	60–213	28–44

noticeable below the apex of the pinna or pinnule and it is this to which the character states in Table 2 refer. The teeth or lobes each have a lateral vein running to the point, and (except in *Christensenia*) the sori occur over these veins in the fertile fronds. Millay (1976, 1979) reconstructs species of *Scolecopteris* a) with apparently fibrous lobes between or corresponding in position to the synangia (e.g. *S. saharensis* Millay, *S. calicifolia* Millay, *S. latifolia* Graham), and b) with more lobes than sori (e.g. *S. mamayi* Millay). In the fibrous forms, the lobes appear to be composed of 'very elongate thick-walled cells of the pinnule hypodermis'. In these the lobing is not easy to compare with that of extant Marattiales but their fibrous construction may have some interest in relation to development of fibre bundles. A toothed lamina margin (character 37) is considered plesiomorphous because it is associated with the least reduced aerial complexes of Ophioglossales (though seen only in certain species of *Botrychium*). The fertile structures of Ophioglossales are such that character 38 (*fertile pinnae or pinnules*: barely recurved → recurved fully to protect sori) cannot be applied to them. The fully recurved state is considered derived based on comparison within Marattiales.

Macroglossum, most species of *Angiopteris* and a few of *Archangiopteris* all have 'fibre' bundles (character 39). (The report of their occurrence in *Marattia squamosa* is erroneous, see Alderwerelt, 1911). These bundles, about five cells wide, are composed of elongate, sometimes thick-walled cells and run parallel to and alternate with the veins of the lamina. Mettenius (1856) accurately described their composition and criticised the still prevalent use of '*nervi* (or *venuli*) *recurrentes*' (recurrent nerves) since they do not show any connection to the lateral veins. When their occurrence is not obvious as a dark line, visible from the lower surface of pinnules, a longitudinal cross-section of the pinnule lamina shows whether they are present or absent.

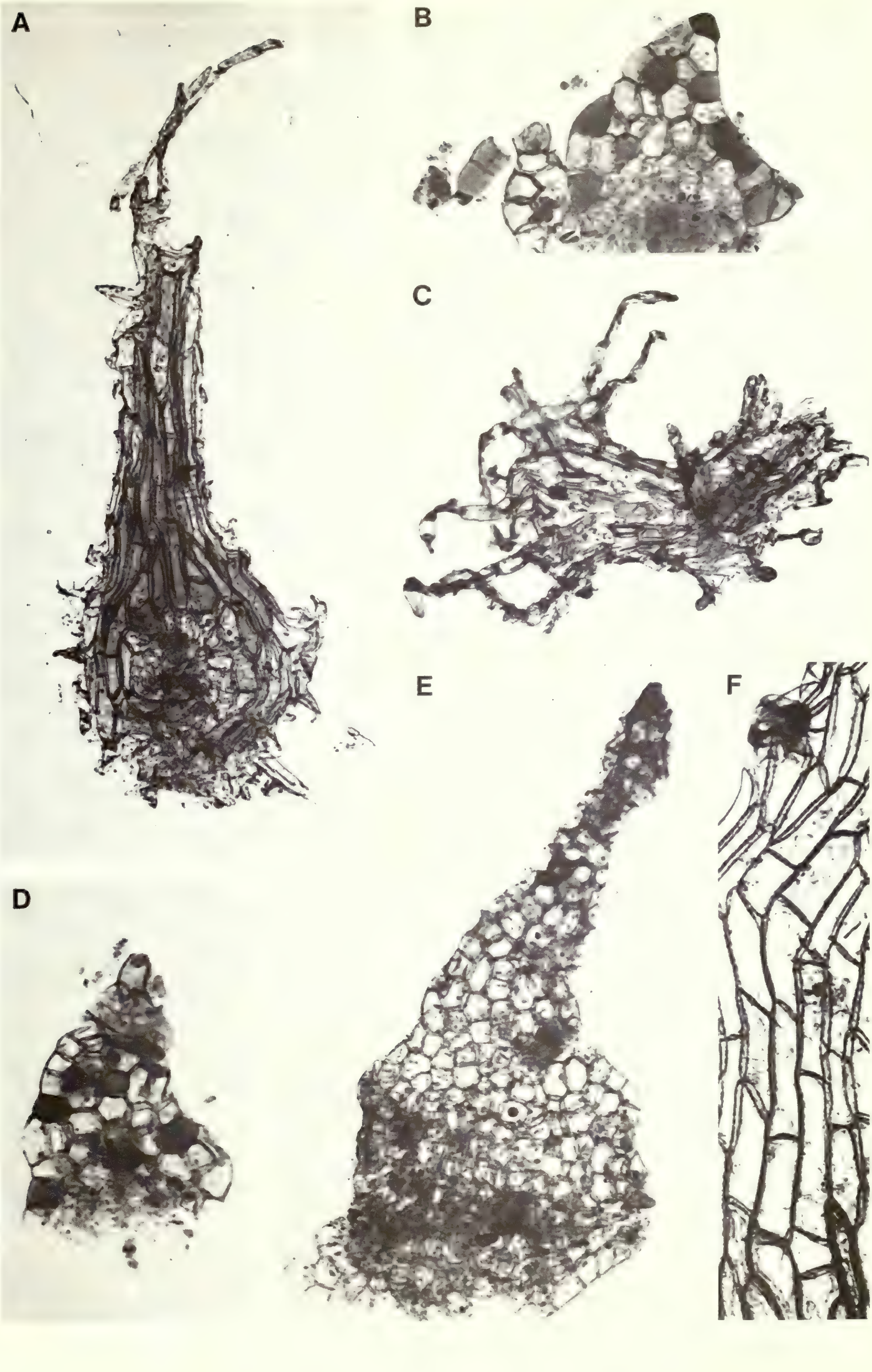
Holttum (1955) writes that the structure of these 'recurrent veins . . . is the same as that of the edge of the leaflet, and apparently they indicate that once *Angiopteris* had fronds more finely divided, but the finer divisions have joined together, the edge-character persisting at the junctions'. Holttum's statement implies that margins of the pecopterid pinnules of *Scolecopteris* show an identical structure to fibre bundles, possibly by reference to the tissue of enlarged cells at the pinnule margin referred to as 'hydathodes' by Scott & Holden (1933). If so, there is in fact no close similarity to fibre bundles and Holttum's view is difficult to understand. We have seen a few of these fibre bundles extending from sinuses of pinnule lobes in a partially tripinnate specimen of *Marattia purpurascens* De Vriese (*Rawson* 1998, Ascension Island [BM]). The cells of these (as in other extant species) are not, however, identical with any of the cells of the pinnule margin.

Hill, Wagner & El-Khayal (1985) have described *Qasimia*, a dimorphic *Marattia*-like fern with mainly taeniopteroid pinnules, from the Permian of Saudi Arabia. It may possibly explain the origin of fibre bundles more accurately. The vegetative fronds of *Qasimia* have more than twice the concentration of lateral veins seen in the fertile ones (the veins being correspondingly more densely forked in the vegetative pinnules). Interestingly, only the fertile pinnules appear to show fibre bundles between the veins. This suggests that the apparent fibre bundles of *Qasimia* represent merely vestigial ordinary vein branches that were surplus to the number needed to service the synangia in fertile pinnules. Thus they would not directly represent evidence of fusion from a more divided ancestral frond. In Mesozoic *Marattia*, which may be regarded as directly descended from *Qasimia*, fibre bundles occur both in the vegetative and fertile pinnules, whilst extant *Marattia* scarcely shows them at all.

Fibre bundles do not occur in Ophioglossales and are therefore interpreted as apomorphous for Marattiales.

40–43. *Scales* (Fig. 11). In both *Christensenia* and *Danaea* the cells in surface view of the scale are more or less isodiametric, but those of *Christensenia* are considerably deeper than those of

Fig. 11 Frond scales: illustrating cell shape and scale margin (characters 40–43). **A**, *Archangiopteris henryi* var. *somai* (Hayata) Tagawa, *C. M. Kuo* 6700, Taiwan (BM). × 50. **B**, **D**, *Christensenia aesculifolia* (Blume) Maxon, *A. C. Jermy* 8316, Philippines (BM). × 75. **C**, *Danaea elliptica* Smith, *A. C. Jermy* 10864, Trinidad (BM). **E**, *Danaea alata* Smith, *A. C. Jermy* 10936, Trinidad (BM). × 50. **F**, *Marattia fraxinea* Smith, *Newman & Whitmore* 475, Malawi (BM). × 50.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Danaea, appearing box-like under the microscope (character 41). In *Marattia, Macroglossum, Angiopteris, Archangiopteris*, and *Protomarattia* the scale cells are elongate and shallow, the cells appearing very thin under the microscope. The lobed margin of *Christensenia* scales is markedly different from the characteristically fimbriate margin of scales of the other extant genera.

Scales of *Scolecopteris* and *Psaronius* are very varied. They include multiseriate 'hairs' (Scott & Holden, 1933; Millay, 1979) which are here termed scales. Scott & Holden also described larger scales which are very thin and expanded, with a microscopically toothed margin much like that of scales of extant Marattiales (Fig. 11F). Stidd (1971) describes more substantial scales with dominantly multicellular transverse sections but which appear also to be expanded, at any rate towards their apices, and there become only one cell-layer thick. The massive, more or less conical appendages on a young sporophyte of *Psaronius* (Stidd & Phillips, 1968) are better referred to as spines.

In extant Marattiales the larger scales often have a podium at the base and (particularly in *Christensenia*) are multicellular in transverse section for some way above this. Millay's (1979: pl. 17, fig. 119) 'scales' seen on the pinna axis of *Scolecopteris mamayi* look remarkably like the podia of *Christensenia*.

Scales are not known in Ophioglossales. Presumed transition from simple to complex has been used to determine the plesiomorphous vs apomorphous states of characters 40–43.

44. *Uniseriate multicellular hairs.* Scott & Holden (1933) figure these on pinnules of *Scolecopteris oliveri*, and their occurrence in *Scolecopteris* is also noted by Millay (1979) and by Stubblefield (1984). Amongst extant Marattiales they occur on the abaxial surface of the lamina of *Christensenia* and *Archangiopteris hokouensis*. Hairs are characteristically lacking from the 'aerial complexes' of Ophioglossales. Their occurrence is taken to be the derived character state mainly on the basis of absence (plesiomorphous) → occurrence (apomorphous).

45, 46. *Veins of lamina.* The usual venation type seen in the least reduced species of Ophioglossales is open dichotomous with reticulate venation in *Ophioglossum* which is considered reduced. Therefore reticulate and occasionally anastomosing veins are considered derived character states.

47. *Sterile and fertile fronds.* Bierhorst uses the non-commital term 'aerial complex' for the 'fronds' of Ophioglossales. If interpreted as true fronds (see Bierhorst, 1971, for discussion) their pinnae are strongly dimorphic, though the least so in species of *Botrychium* such as *B. virginianum*, considered by us the most plesiomorphous members of the order. Comparison is difficult with Marattiales even on this basis, since it is generally whole fronds of Marattiales rather than their pinnae that are dimorphic. We have chosen (for simplicity) to polarise the states of this character solely with reference to extant Marattiales, thus regarding dimorphism as relatively apomorphous for the order.

Note on characters 48–68. For many of these characters Ophioglossales provide no useful guidance for determining the polarity of character states. They do not in general have sori (the nearest analogue to Marattiales being the 'synangium' of *Ophioglossum*) and in all cases each sporangium has its own vascular supply, even in *Ophioglossum* (Bierhorst, 1971; Sporne, 1975). As a result, this group has nothing that could be homologised with the placenta of Marattiales or Filicales. The polarity of the states of characters 48, 50–56, and 62–67 has therefore been determined by comparison amongst Marattiales.

Figure 12 illustrates the terms used for discussion of characters 48–52 and 57–66.

48–49. *Placental hairs and synangial scales.* Presl (1845) segregated genera within *Marattia* partly on the presence or absence of an 'indusium' – a term applied wrongly to Marattiales and

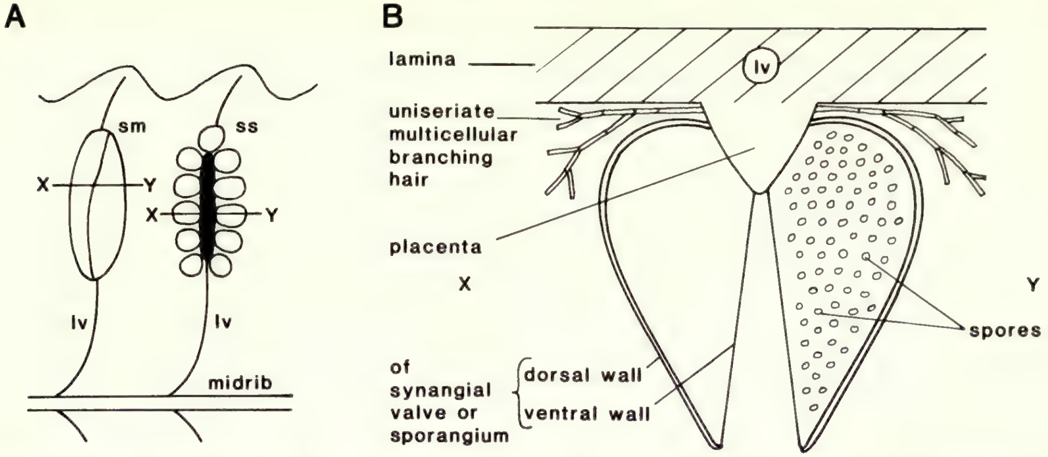

A
sm
ss
X
Y
X
Y
lv
lv
midrib
B
lamina
lv
uniseriate multicellular branching hair
placenta
X
Y
spores
of synangial valve or sporangium
dorsal wall
ventral wall

Fig. 12 **A**, Plan of undersurface of an idealised fertile pinnule of Marattiales; sm, synangium; ss, sorus of separate sporangia; lv, lateral vein. The lines X–Y indicate the plane of the vertical section shown in B. **B**, Vertical section through a generalised marattialean sorus or synangium, illustrating terms used for discussion of characters 48–52 and 57–66, in particular 'dorsal' vs 'ventral' wall and 'placenta'.

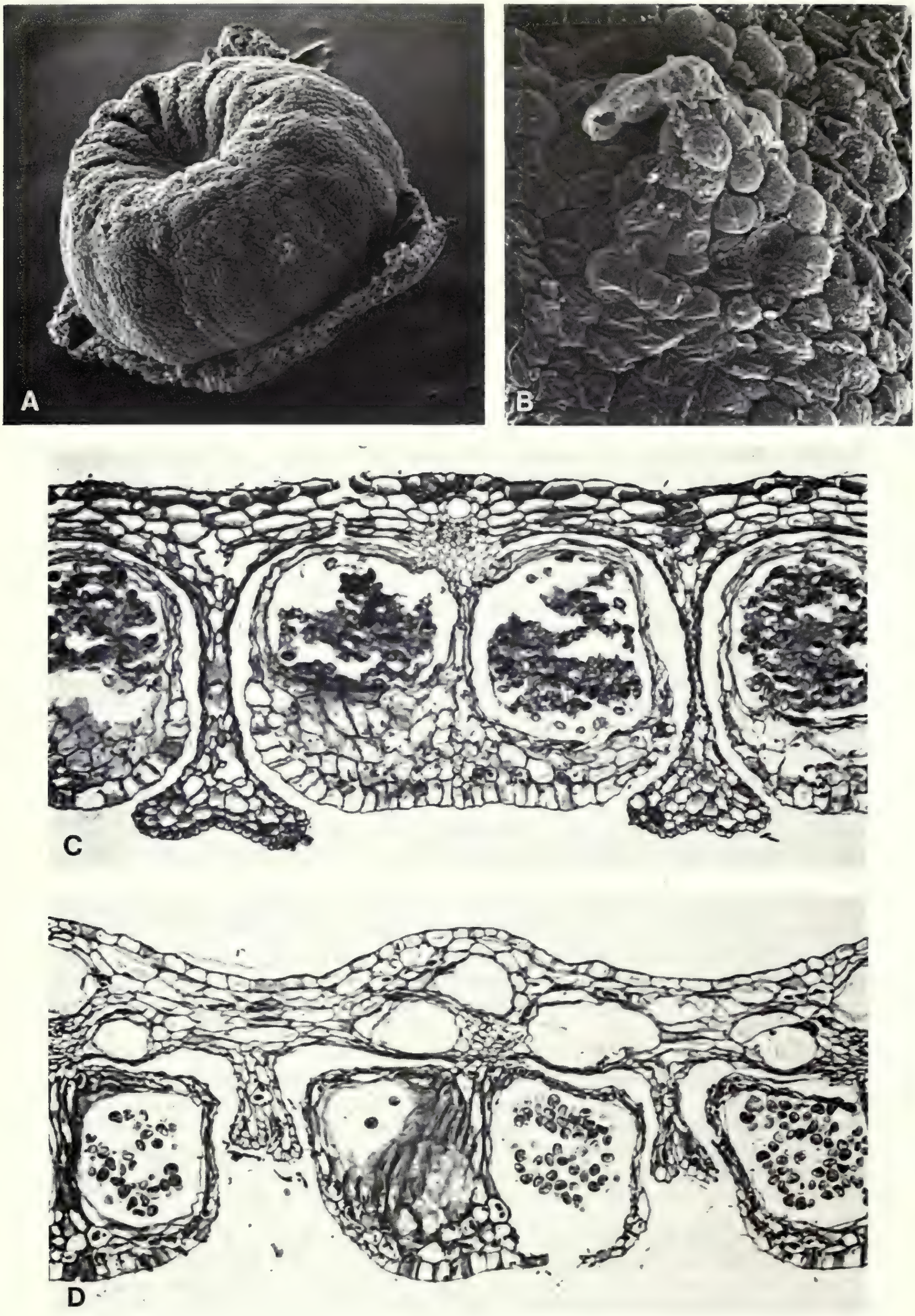
referring merely to the hairs attached to the placenta. Mettenius (1856) was the first to criticise this misuse of the term. Ching (1958*a, b*) referred to the hairs as paraphyses or paraphysate hairs, as did De Vol (1973) and Holttum (1978). Mettenius (1856) pointed out that Presl's concept of these hairs as always present or absent in a species was incorrect. More recently, Bienfait (1968) concluded that as well as their presence or absence depending on the age of the specimen examined, it also depended on the ecological or geographical 'forms' or 'races' studied. We have recorded great variability in development of placental hairs in successive fronds of a specimen of *Angiopteris evecta* growing at K (*Birdsey* B, Pahang, K hort. 371–77.02808). Millay (1976) comments on *Scolecopteris* 'the quantity of hairs present on any given specimen varied widely, and is thought to reflect environmental influences'. Chang (1975) and Holttum (1978) consider the degree of branching of the placental hairs may be a useful character at the specific level.

In *Danaea*, scales (rather than hairs) occur on the walls of the lamina troughs that envelop the synangia, but they are not found on the placenta.

Uniquely amongst extant Marattiales, we have found that *Christensenia* has scales on the dorsal wall of the synangium (Fig. 13A, B). These synangial scales are easily shed, and commonly only the slightly protruding region of attachment is seen. Millay (1976, 1979) found uniseriate multicellular hairs on the sporangial wall of eight species of *Scolecopteris* and multiseriate as well as uniseriate hairs on those of *S. saharensis* and *S. mamayi*. His illustration of *S. mamayi* (1979: pl. 17, fig. 116) suggests that the 'multiseriate hairs' are referable to scales.

Fig. 13 **A, B**, *Christensenia aesculifolia* (Blume) Maxon, *A. C. Jermy & J. M. Rankin* 14907, Sabah (BM): scales on dorsal wall of synangium (character 49). The synangia were rehydrated in 10% commercial bleach ('Domestos'), then critical point dried. SEM photographs. A × 20. B, Detail of scale from another synangium of same specimen as in A. × 150. **C, D**, Vertical sections of synangia of *Danaea* showing lamina between synangia 'expanded' to varying degrees (character 50). **C**, *Danaea alata* Smith, *C. Wright* 1066, Cuba (BM). × 60. **D**, *Danaea nodosa* (L.) Smith, *A. F. Skutch* 4180, Costa Rica (BM). × 60.

Fig. 14 Tracheids in placental tissue of synangium (character 51). **A, B, D**, *Marattia laevis* Smith, *J. Miers* s.n., 1840, sine loc. (BM). A, Vertical section through a synangium. × 40. B, D, Detail of tracheids from a successive serial section to A. B × 150. D, Close up of B. × 400. **C, E**, *Christensenia aesculifolia* (Blume) Maxon, *Griffith* 1696, Assam (BM): vertical section through a synangium. × 20. F, Tracheids at base of synangium (arrowed in C). Interference contrast. × 600.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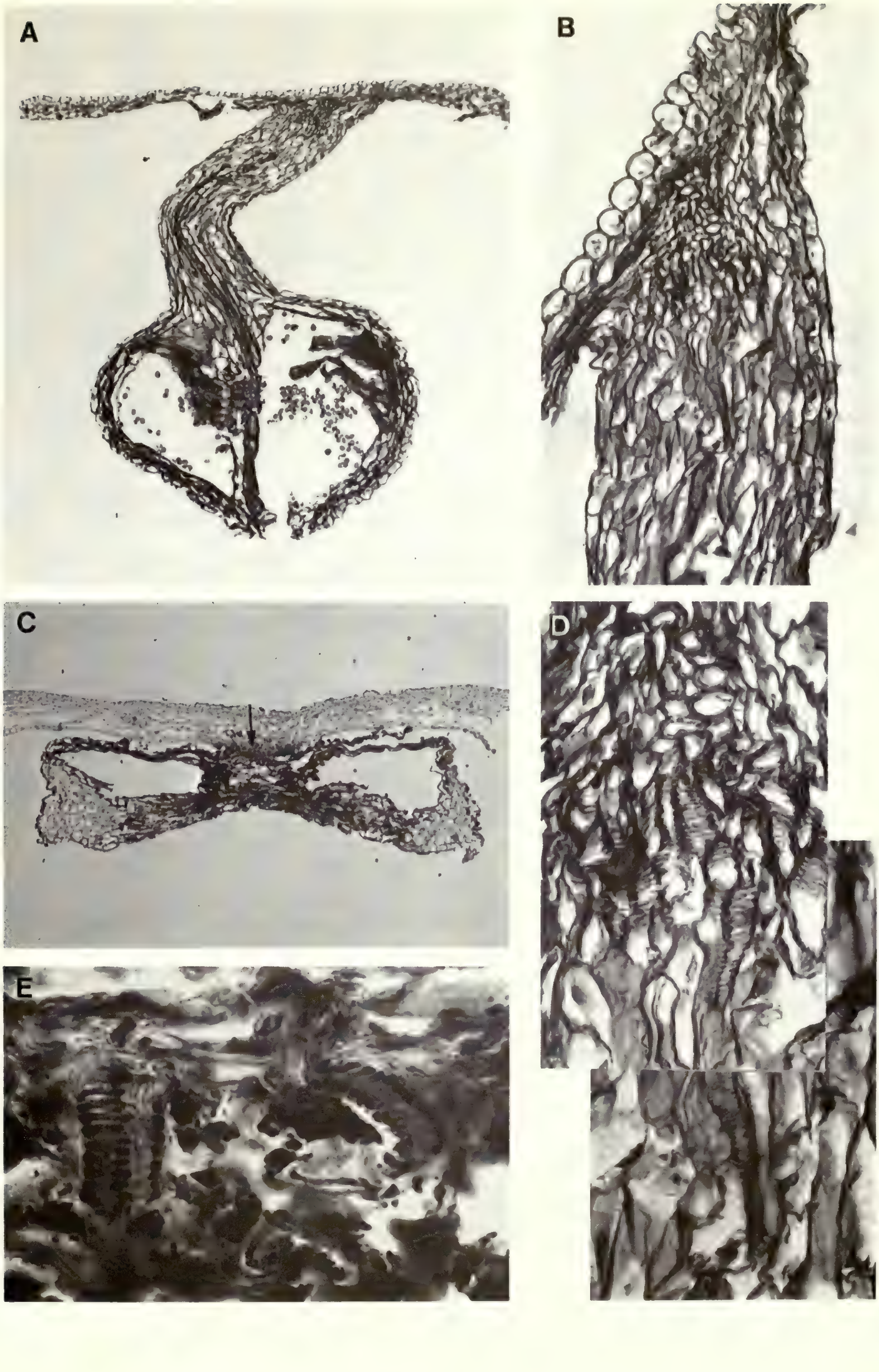
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50. *Expanded lamina tissue between sori.* This interesting feature of *Danaea* is illustrated in Fig. 12C, D. It also occurs, but to a lesser extent, in *Scolecopteris mamayi* (Millay, 1979) and in extant *Macroglossum* and *Angiopteris elliptica*. In the fossil *Millaya* Mapes & Schabilion (1979*b*) the expansion is as strongly marked as in *Danaea*.

We do not consider the expanded lamina tissue of Marattiales to be homologous with the intersporangial tissues of *Ophioglossum* (Bierhorst, 1971).

51. *Tracheids in placental tissue.* Millay (1979, 1982*a*) has observed fibres and tracheid-like elements with scalariform thickening in the pedicellate placenta of some species of *Scolecopteris*. (He (1982*b*) appears to indicate that *S. conicaulis* Millay has fibres rather than tracheids.) Millay regards all such elements in the placenta – whether fibres or tracheids – as primitive, based on interpretation of the synangium as a fertile telome truss (Zimmermann, 1952). To this extent the argument for polarity, whilst reasonable, rests as much on palaeontological evidence and preconceptions as on character comparison, though to the extent that Ophioglossales have vascularised axes bearing the sporangia, Millay's view may be considered to receive general support from character comparison. We have adopted the reverse polarity, based solely on character comparison within Marattiales. Figure 14A, B, D, shows short tracheids in the pedicellate placenta of extant *Marattia laevis*, comparable to those of *Scolecopteris* and (so far as we know) reported for the first time in this paper.

In *Christensenia* there is a peculiar disc of such cells, at the base of the central column only, with no clear connection to the underlying vein (Fig. 14C, E) (originally figured, but not commented on, by Luerssen, 1875*a*).

53. *Development of placenta.* The pedicellate placenta (receptacle) of some extant species (Figs 14C, D; 17A, C) shows a remarkably close resemblance to the 'pedicel' of *Scolecopteris* (Millay, 1979, 1982*a*; Stubblefield, 1984).

55–56. *Arrangement of sori.* Mettenius (1856) writes that *Kaulfussia (Christensenia)* bears synangia in an approximately biseriate manner (character 56, illustrated in Fig. 15B). The developmental sequence of frond form (Fig. 7) has been separated by some authors into two species of *Christensenia, C. cummingiana* Christ and *C. aesculifolia* s.s. The distribution of synangia in *Christensenia* may be linked with apparent 'concertina-reduction' of the frond from fundamentally pinnate to approximately palmate. In the other extant genera, the sori typically occur in two rows parallel to the midrib (Fig. 15A).

57. *Position of sori relative to margin.* A phyletic slide in the position of sori on the lamina was proposed by Bower (1926), from marginal to superficial, but Wagner (1973) does not include soral position in his table of 'Directionality of character states'. *Danaea* and some species of *Archangiopteris* have long sori that cover almost the full width of the lamina. They seem to differ. In *Danaea* the inner ends of the sori form a uniform line near the midrib and the sori extend for varying lengths outward towards the pinna margin. In *Archangiopteris* the converse arrangement occurs: the outer ends of the sori form a uniform line near the margin and the sori extend for varying lengths inward, towards the midrib (Fig. 16). However, this is a tendency only, which seems slightly stronger in *Archangiopteris*.

58. *Symmetry of sorus in plan view.* Whilst typically round in *Christensenia* and elongate in the other extant genera, abnormal radial synangia or sori occur occasionally in *Danaea, Marattia,* and *Angiopteris* and somewhat elongate ones in *Christensenia*. They mutually counteract any taxonomic value that might be placed on them.

59. *Packing together of spore-bearing loculi of synangia (or sporangia of sori).* The close packing of sporangia in the sorus (or of the synangial loculi) is unique to Marattiales amongst the ferns (see p. 272 for discussion).

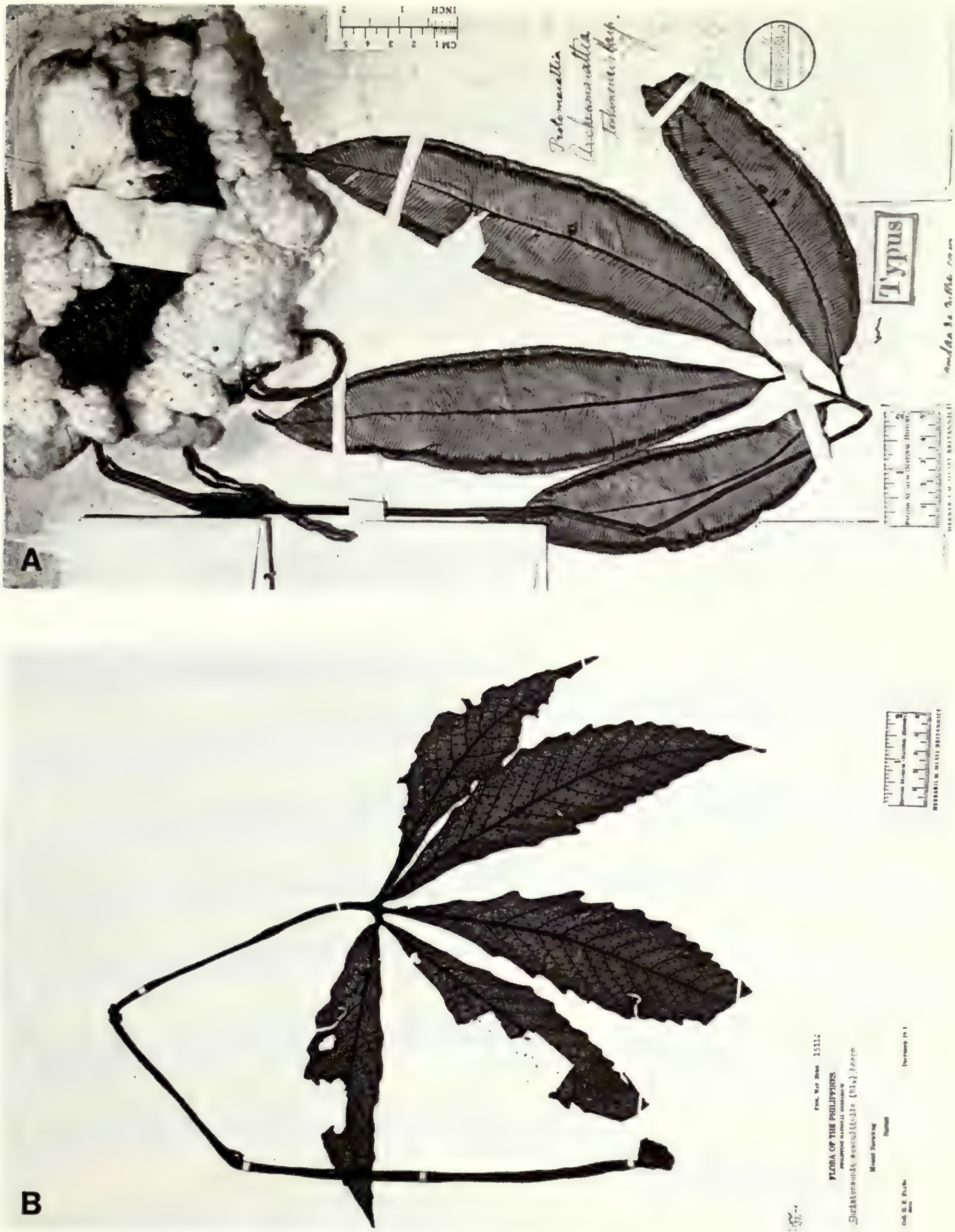


Fig. 15 Arrangement of sori (character 54). **A**, *Protomarattia tonkinensis* Hayata, *Hayata* s.n., 30 July 1917, Vietnam (TI): sori in two rows which lie parallel to midrib and margin. **B**, *Christensenia aesculifolia* (Blume) Maxon, *G. E. Edaño* 15112, Philippines (BM): sori mainly in two rows, the rows parallel to the main lateral veins rather than midrib and margin.

60–62. *Cell differentiation in sporangial or synangial walls.* Stomata are not seen in the sporangial or synangial walls of any extant Marattiales or Ophioglossales, contrary to the frequently quoted statement of Eames (1936) e.g. by Sporne (1975). Nor have they been seen with certainty in these structures in *Scolecopteris* (Scott, 1932; Millay, 1979, 1982*a*, *b*).

Millay has studied the reproductive structures of *Scolecopteris* species in detail, based on peel sections of permineralised material. For some characters the range of variation he describes

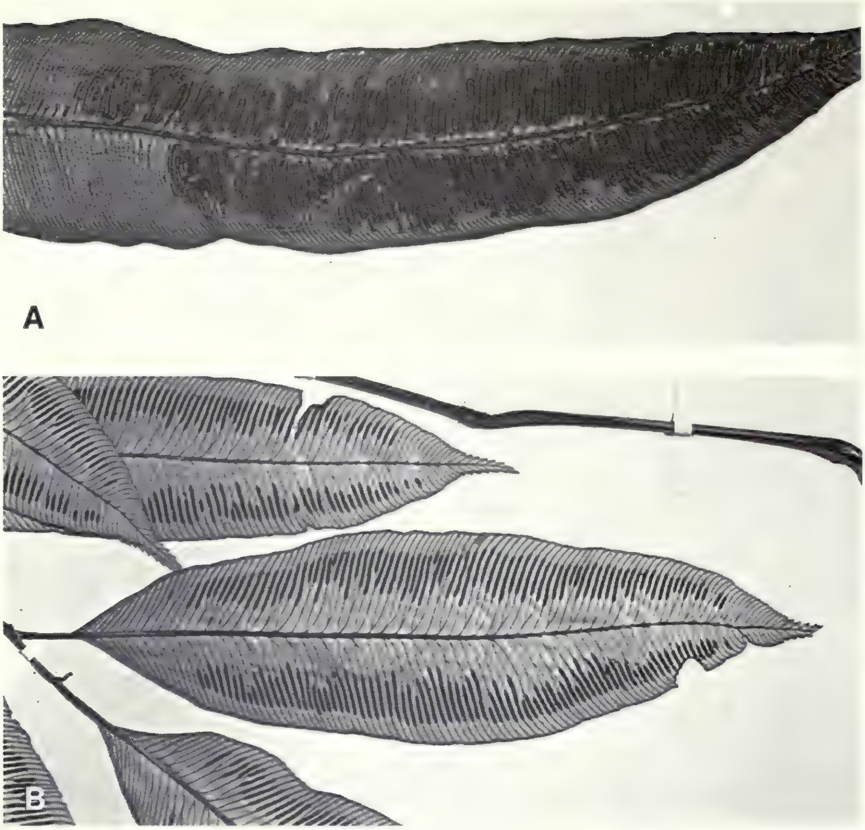


Fig. 16 Arrangement of sori. **A**, *Danaea nodosa* (L.) Smith, *A. Hombersley* 240, Trinidad (BM). × 1. **B**, *Archangiopteris henryi* Christ & Giesenh., *Henry* 11544A, Yunnan (BM). × 0·5. In *Danaea* the inner ends of the sori form a uniform line near the midrib and the sori extend for varying lengths outwards towards the pinna margin. In *Archangiopteris* the converse arrangement occurs: the outer ends of the sori form a uniform line near the margin and the sori extend for varying lengths inwards towards the midrib.

occurs also to some extent in extant Marattiales. For example, sporangial/synangial apices may be long or short, blunt or acute, though the range is smaller in the extant species. The ratio of the height of the placenta to the height of the sporangium/synangium may be low or high, which is very similar to that of the extant taxa. Some species of *Scolecopteris* are similar to extant species of Marattiales in the number of layers of cells in the dorsal wall of the sporangium or synangium, but there is greater variation in the detailed structure of this dorsal wall than in extant Marattiales. For example, in *S. parvifolia* (Mamay) Millay and *S. majopsis* Millay there is a middle layer of cells with thickened walls. However, a layer of thickened cells below the outermost layer of cells may also occur in the dorsal wall of *Marattia costulisora* Alston, *M. werneri* and *M. rolandi-principis*, as indicated by sections made from rehydrated herbarium specimens (Fig. 17A, B), but the quality of the rehydration is far from perfect and this requires checking from fresh material.

The extant species examined for this study have some characters not described by Millay (1979, 1982*a, b*) for all *Scolecopteris*. These may well prove to be very useful at the subgeneric level. For example, in *Angiopteris* the outermost cells of the dorsal wall may be elongate, similar to those of the ventral walls, or almost isodiametric (Fig. 18B, D). Where isodiametric, the outer periclinal walls may bulge out conspicuously as in other genera. In *Marattia* the shape of the surface cells of the inner-facing walls of the synangial valves can be strikingly different from one

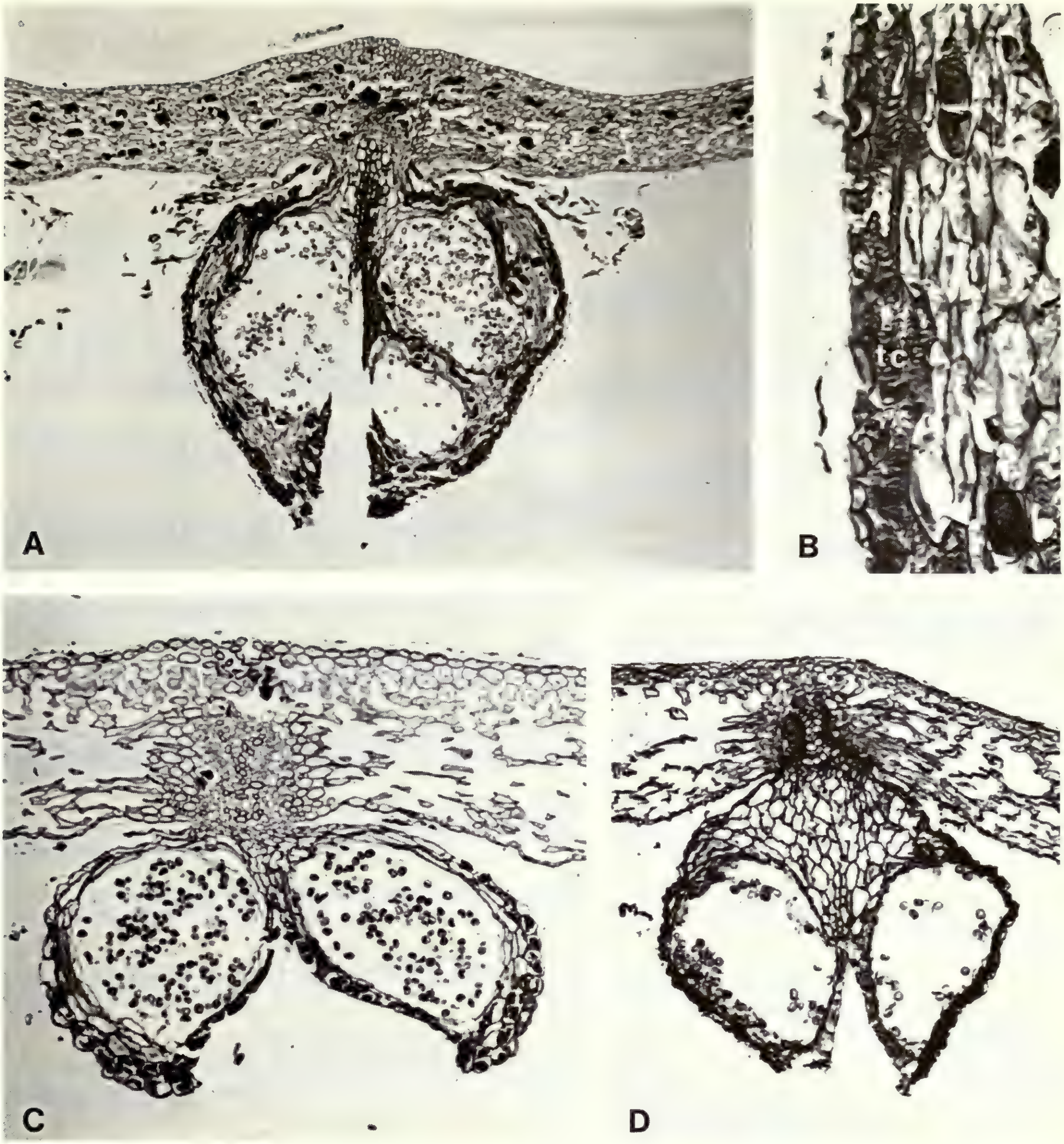


Fig. 17 **A**, *Marattia costulisora* Alston, *Clemens* 5157, New Guinea (BM): vertical section through a synangium, obliquely so of right hand valve. × 40. **B**, Detail of A showing cells with apparently thickened walls in dorsal wall of synangium (tc). × 200. **C**, *Archangiopteris henryi* Christ & Giesenh., *Henry* 11544A, Yunnan (BM): vertical section through sorus. × 50. **D**, *Protomarattia tonkinensis* Hayata, *Hayata* s.n., 30 July 1917, Yunnan (BM): vertical section through sorus. × 50.

species to another (Fig. 18A, C). Our sections of synangia of *Marattia fraxinea* Smith and *M. werneri* show scattered cells in the outermost layer of the dorsal wall, the contents of which resemble those of the idioblasts of the lower epidermis (character 36). In *Archangiopteris* and *Angiopteris* the arrangement of the apical thickened cells can differ markedly in different species.

Our concept of the outermost cell layer in a generalised *Angiopteris* sporangium, based on comparison amongst extant Marattiales and Ophioglossales (see p. 285), is one with a rounded apex with thick-walled, more or less isodiametric cells; outermost cells of the upper half of the dorsal wall more or less isodiametric with thin periclinal walls which bulge outwards; cells of the

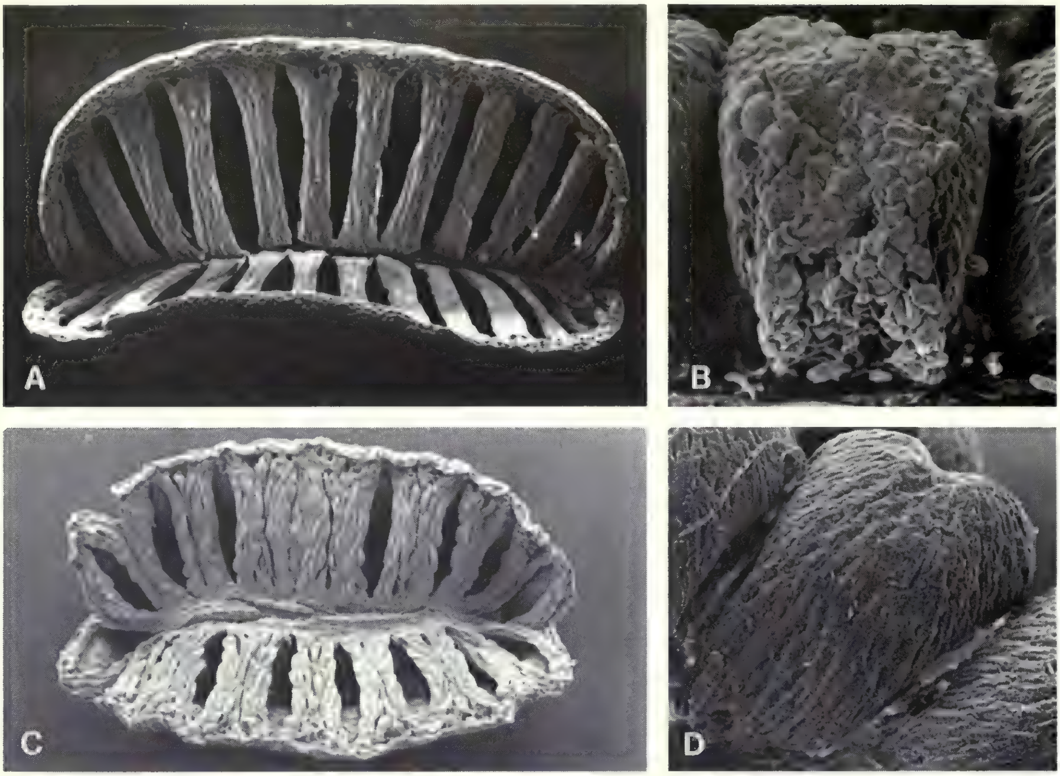


Fig. 18 Variation in surface layer of cells of dorsal and ventral walls of synangia and sporangia. **A**, *Marattia brassii* Copel., *L. J. Brass* 12117, Irian Jaya, New Guinea (BM). × 35. **B**, *Angiopteris laciniata* Vriese, *E. Smith* 2208, Thailand (BM). × 100. **C**, *Marattia alata* Smith, *D. Moore* s.n., Jamaica, 1857 (BM). × 50. **D**, *Angiopteris ankolana* Vriese, *Junghuhn* 698, Sumatra (BM). × 100. SEM photographs.

ventral wall elongate and parallel to the dehiscence slit. The characters of *Scolecopteris* described by Millay (1979, 1982*a, b*), other than to some extent for *S. minor* Hoskins emend. Millay, and some other species do not appear, however, to correspond to this.

In Ophioglossales the surface cell layer of the sporangial wall is composed uniformly of more or less isodiametric cells. The cells of the ventral walls of the sporangia are aligned parallel with the dehiscence slit and there is no group of more or less isodiametric, thick-walled cells at the apices of the sporangia. The polarity of characters 60–62 was decided by comparison with this group, partly because Psaroniaceae shows an unhelpfully wide range of variation of these characters in this context. We note, however, that 'trimerophytes', in contrast to Ophioglossales, had elongate more or less pointed sporangia and the surface cells of the wall were elongate (Stewart, 1983).

63. *Number of sporangia or locules per sorus or synangium.* This is not a constant character, even allowing for those taxa in which the sori almost cover the lamina width. An extreme example is the individual of *Angiopteris evecta* mentioned under character 48 above, where an average of seven sporangia per sorus was found on one frond and sixteen on the successive frond. In *Christensenia* (and possibly other taxa) a bimodal score obtained for the number of locules in the synangium might be considered to reflect polyploidy, although we did not obtain such a score for the cytological voucher specimens referred to for character 34.

Our observations show a marked difference in placenta height of different individuals assigned to *Marattia fraxinea*. Millay (1976) also points out a difference in height of synangia in different 'species' of *Christensenia*.

64–69. *Partial or complete lateral fusion of the dorsal or ventral walls of the sporangia (and dehiscence).* Fusion is interesting in relation to whether the free sporangiate or the synangiate state should be considered the generalised condition for Marattiales. Early work by various authors on the ontogenetic development of marattialean sporangia is summarised by Bower (1898), with more recent studies by Bienfait (1969) and Bierhorst (1971). Bienfait considered that *Angiopteris* shows a tendency towards being synangiate whilst Bierhorst concluded that the free sporangiate condition is the derived one. As both synangiate and free sporangiate forms are found in *Scolecopteris* and other relevant fossils of Carboniferous age, palaeontological evidence has not been used by the various authors to determine polarity. In this study we have initially chosen as a compromise to consider the partially fused state to be generalised by using outgroup comparison with *Psaronius* + *Scolecopteris*, but our overall results refute this choice for the extant genera (p. 289).

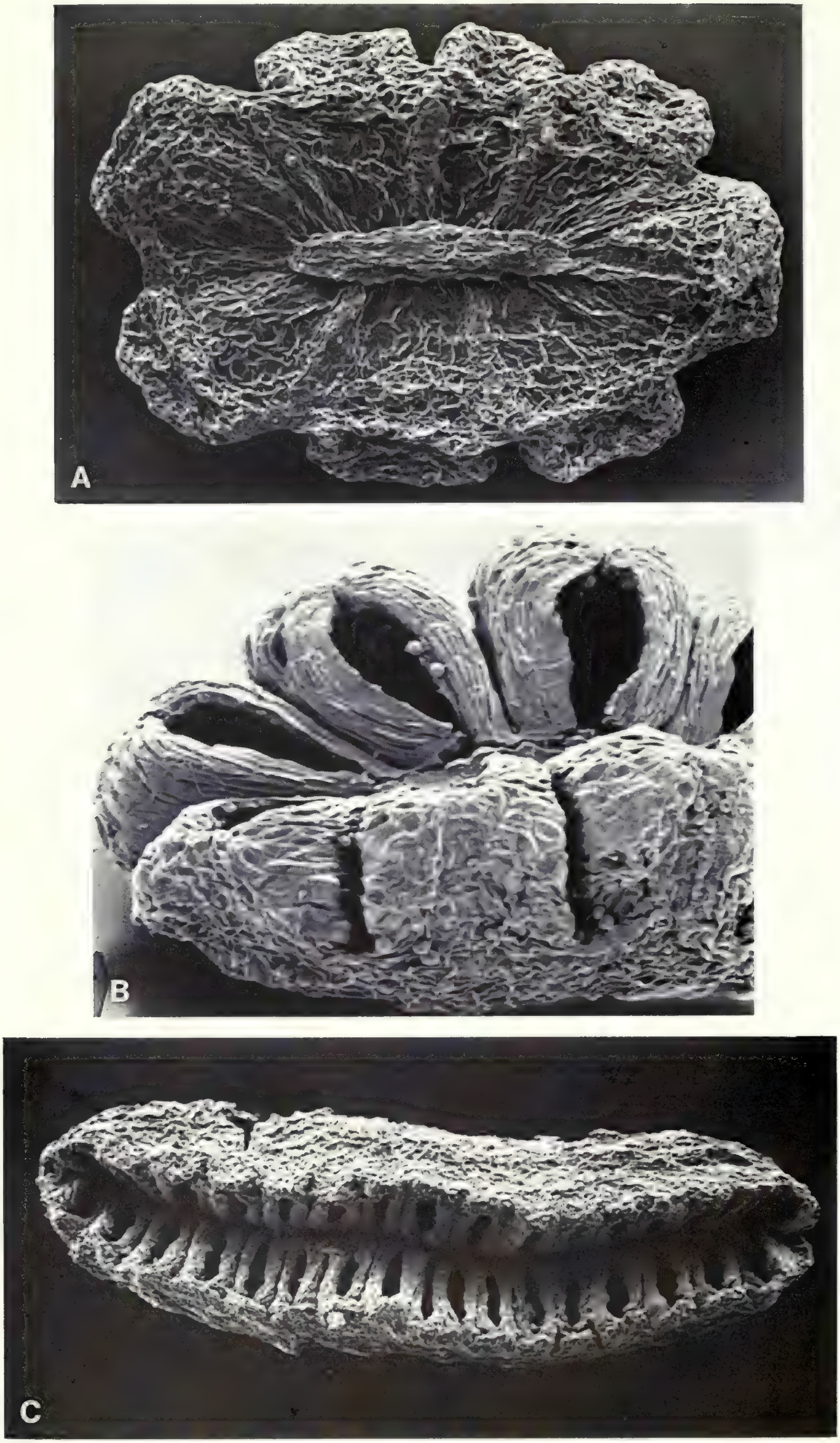
Millay (1976) observed that sporangia of *Angiopteris crassipes* Wallich and *A. faurieri* Hieron. may be fused laterally at the base. This feature has also been seen by us in *Angiopteris fokiensis* Hieron., *A wallichiana* C. Presl (Fig. 19A, B), *Archangiopteris cadierei* (*Cadière* C, Vietnam [P]), and *A. caudata* (specimens ex Herb. Kwangsi University, Southern Kwangsi [PE]). We consider these mostly to be abnormalities. Presumably because he did not see such fusion in *Archangiopteris*, Millay (1976) writes that its sporangia are truly free, comparable to those of *Eoangiopteris* Mamay (Mamay, 1950). He (1976, 1979, 1982*a, b*) interprets the sporangia of *Scolecopteris* as being fused laterally for part or all of their length prior to dehiscence, and considers that the sporangia would separate laterally before shedding their spores. If so, this is unlike the extant Marattiales, as is the oblique arrangement of cells associated with the dehiscence slit in at least some species of *Scolecopteris*.

Figure 20 shows the cells of the outer layer of the dorsal and ventral walls of sporangia and synangia in some extant Marattiales, all characteristic species of each genus. The photographs are of herbarium material rehydrated with 10% ‘Domestos’ and stained with gentian violet or safranin differentiated by brief immersion in ethanol. The thick-walled cells (stained darker) are similar in *Marattia, Angiopteris, Macroglossum, Archangiopteris,* and *Protomarattia*. In *Danaea* the cells around the pore have only their tangential walls thickened in relation to the pore. No such differentiation of cells was seen in preparations of *Christensenia*.

Another feature seen in sori of *Macroglossum, Angiopteris, Archangiopteris,* and *Protomarattia*, apparently also not recorded before, is that the immature sporangia on opposite sides of the placenta are touching, with the ventral walls of the sporangia vertical. Thus they have the same attitude as the two valves of *Marattia* synangia. As they mature they spread apart, the dorsal sporangial walls becoming closer to the lamina before the sporangia finally open. Similarly, the synangia of *Christensenia* seem also to open out prior to dehiscence. It is possible that *Scolecopteris* showed this as well.

70–73. *Spore characters.* Spores of seventy species of extant Marattiales have been examined by Mettenius, 1856; Tchistiakoff, 1874; Jonkman, 1880; Selling, 1946; Harris, 1955; Erdtman, 1957; Ching, 1958*a, b*; Nayar, 1964; Nayar, Lata & Tiwara, 1964; Tardieu, 1966; Welman, 1970; Erdtman & Sorsa, 1971; Lugardon, 1971, 1972; Kremp & Kawasaki, 1972; Bobrov, 1973; M. D. Crane, 1973; Morucchio, 1973; Devi, 1977; Millay, 1976; Huang, 1981; Pant, Misra & Singh, 1982; Tryon & Tryon, 1982 and Pettitt pers. comm. Their surface morphology and structure are described in varying degrees of detail and with varying accuracy. The spores of some of the taxa studied here are illustrated in Figs 21 and 22.

Mettenius (1856) was the first to comment on the occurrence both of long and spherical spores, with mono- and trilete marks respectively, within the synangia of any one plant of *Marattia*. This has been recorded by later authors for *Christensenia, Angiopteris,* and *Archangiopteris*, as well as for *Marattia*. Millay (1979) who has noted this also in *Scolecopteris*, comments that it indicates genetic instability and ‘is by implication a primitive trait’. It has been noted also in Jurassic species by Van Konijnenburg-Van Cittert (1975*a*). The spores often, however, appear alete. M. D. Crane (1973) discusses the occurrence and possible formation of these. He suggests that they may not truly lack some sort of aperture. But very little is known at present of


A
B
C

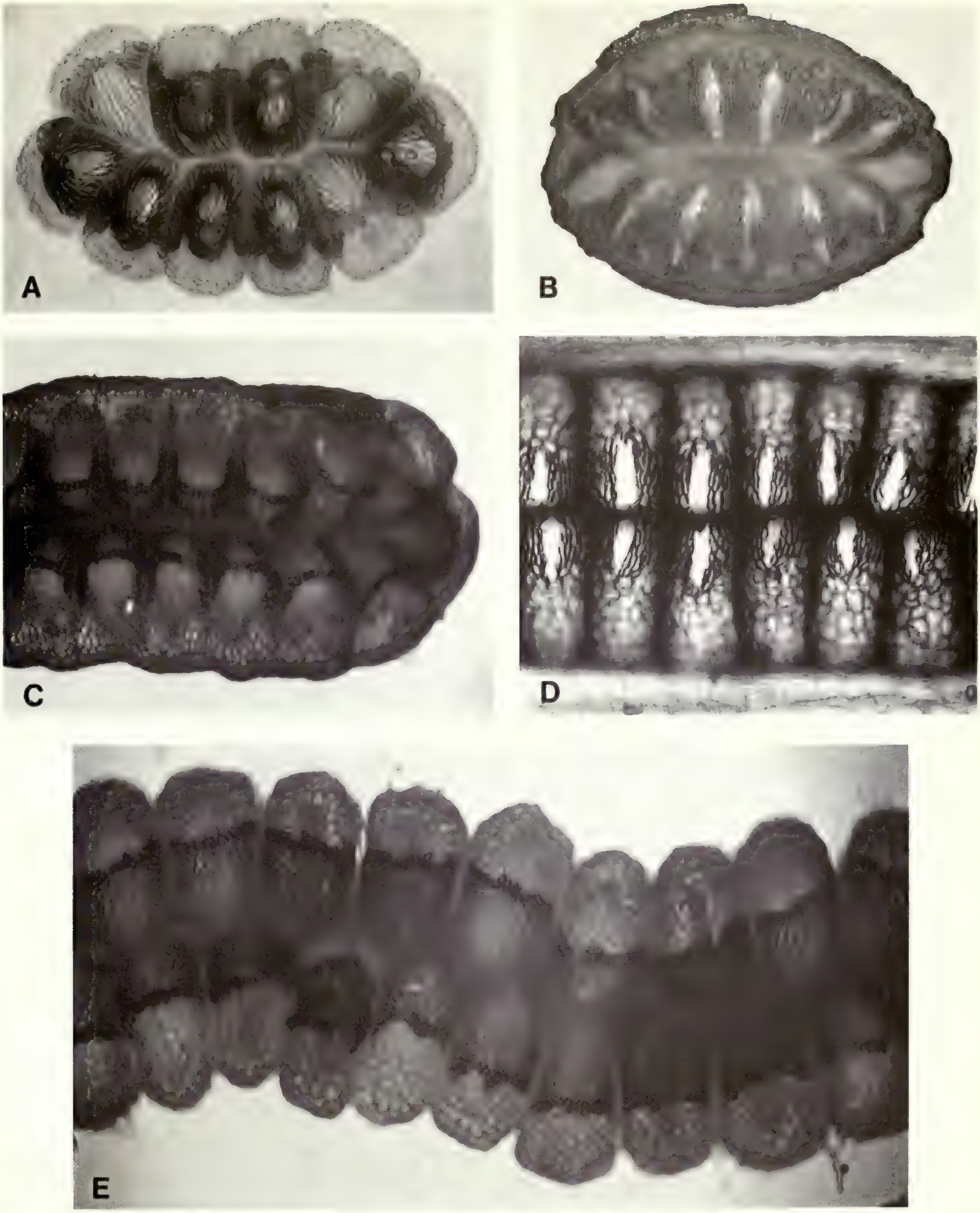


Fig. 19 Fusion of dorsal walls of sporangia (characters 66 and 68). **A**, **B**, Abnormal specimens of *Angiopteris*. **A**, *Angiopteris fokiensis* Hieron., *J. Linsley Gressitt* 589, Kwangtung (BM). × 90. **B**, *Angiopteris wallichiana* C. Presl, Herb. Lacaita 15866, Sikkim (BM). × 150. **C**, *Protomarattia tonkinensis* Hayata, *Hayata* s.n., 30 July 1917, Vietnam (TI). × 40. SEM photographs. Compare with the sections shown in Fig. 16.

Fig. 20 Cell differentiation of surface layer of sporangial and synangial walls. **A**, *Angiopteris evecta* (G. Forster) Hoffm., Leeds University Expedition, s.n., Sri Lanka, (in cultivation at Leeds University Botanic Garden + BM). × 50. **B**, *Marattia alata* Smith, *D. Moore* s.n., Jamaica, 1857 (BM). × 40. **C**, *Protomarattia tonkinensis* Hayata, *Hayata* s.n., 30 July 1917, Vietnam (BM). × 40. **D**, *Danaea nodosa* (L.) Smith, *A. Fendler* 129, Trinidad (BM). × 50. **E**, *Archangiopteris henryi* var. *somai* (Hayata) Tagawa, *Ogata* 1, Taiwan (BM). × 50.

[illegible] the high percentage of deform[illegible] [illegible] of them per sporangium [illegible] [illegible] theory that accounts [illegible] [illegible] considered, like Millay, that thi[illegible] [illegible] tetrad). Outgro[illegible] [illegible] suggests [illegible] [illegible] 1968; Erdtman [illegible]

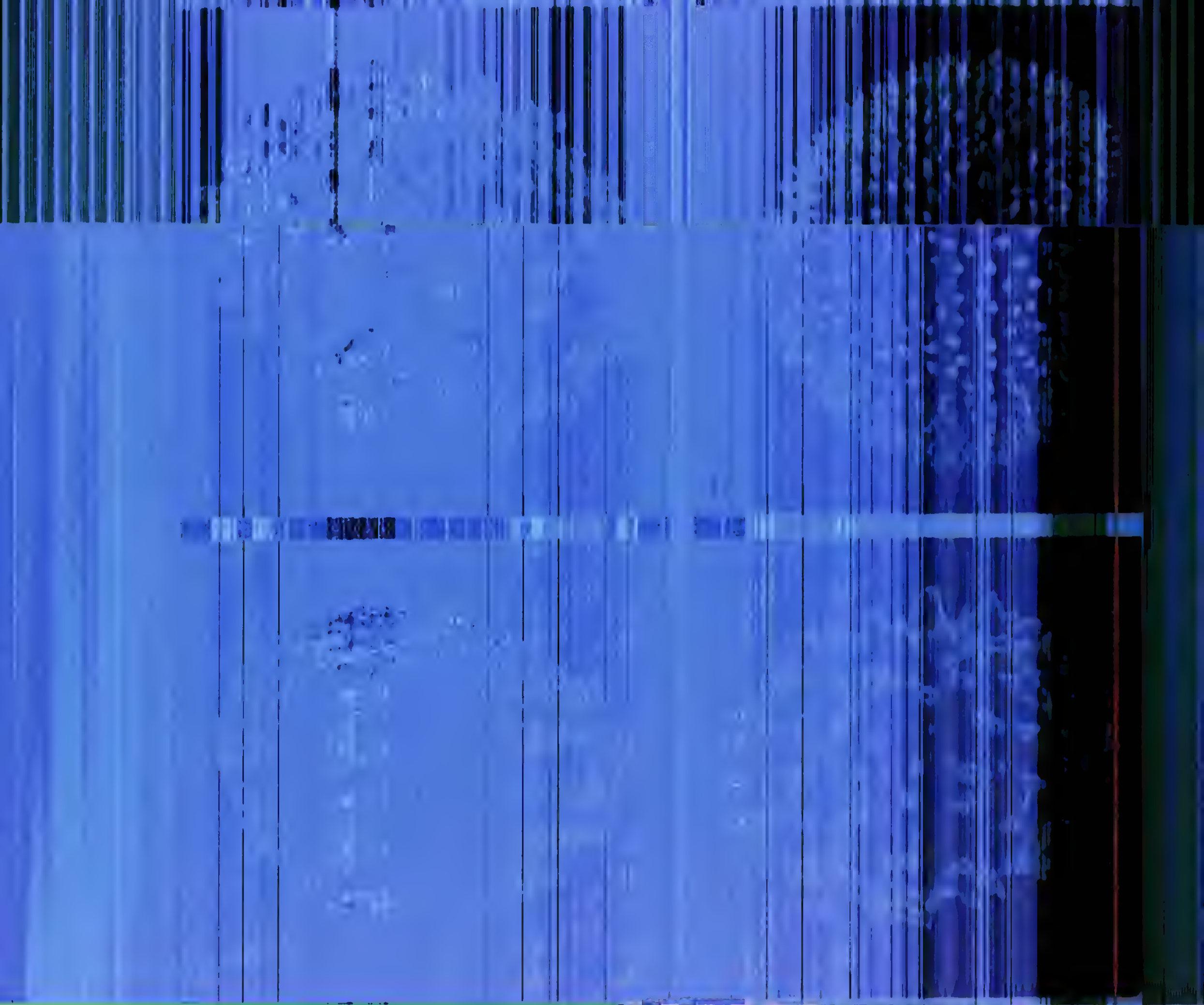
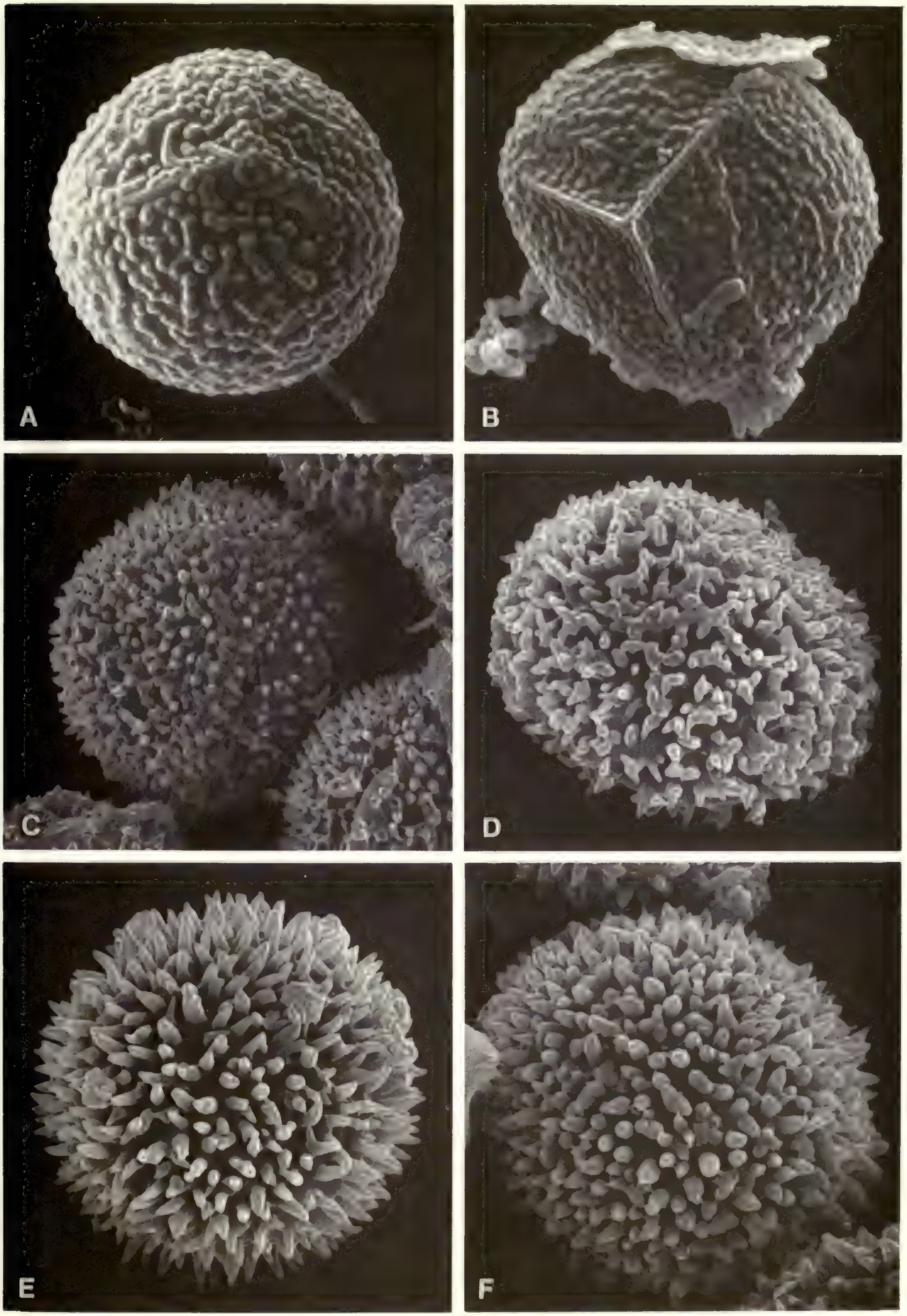


Fig. 21 Spores of extant Marattiales. SEM pho[illegible] (BM). × 2000. **B**, *Christensenia aesculifolia* [illegible] *Marattia fraxinea* Smith, *Verdcourt* 62, Tanzan[illegible] *Hoogland* 9258, New Guinea (BM). × 3000. A[illegible]

Fig. 22 Spores of extant Marattiales. SEM pho[illegible] s.n., (Herb. Copeland 7), Sarawak (MICH). [illegible] *Forster* 438, Society Islands (BM). × 2500. **C**, [illegible] 1917, Vietnam (TI). × 2000. **D**, *Archangiopteri*[illegible] × 2000. **E**, *Archangiopteris tamdaoensis* Haya[illegible] *Archangiopteris cadierei* C. Chr. & Tard., *Cad*[illegible]


A
B
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E
F

Sorsa, 1971; Lugardon, 1971, 1972; Wagner, 1974; Verma & Khullar, 1979; A. F. Tryon, MS). Bierhorst (1971) adopts the opposite polarity.

Millay (1979, 1982*a, b*) has shown that there are two major differences between the spores of *Scolecopteris* and those of extant Marattiales. One is the range of spore size (*c.* 13–88 μm in *Scolecopteris* vs *c.* 20–40 μm in extant genera). The other is the layer of the spore wall that develops ornamentation. Millay (loc. cit.) and Millay & Taylor (1985) consider that in most species of *Scolecopteris* it is the perispore that is ornamented; in a few (*S. majopsis, S. altissima* (Mamay) Millay and *S. alta* (Watson) Millay) it is the exospore. In extant Marattiales it is the exospore that shows ornamentation, though the perispore in *Marattia, Angiopteris, Macroglossum, Archangiopteris,* and *Protomarattia* more or less moulds and therefore replicates the exospore. Such replication of the exospore ornamentation by the perispore is seen in some *Scolecopteris* species (Millay, 1979). In *Danaea* and *Christensenia* it seems that the perispore is only seen as a scant layer between the spines or ridges of the exospore (Tchistiakoff, 1874; Lugardon, 1971, 1972; M. D. Crane, 1973; Millay, 1976; Gomez & Walter, 1980; Pettitt pers. comm.).

T.E.M. work on extant Marattiales and Ophioglossales (Lugardon, 1971, 1972) shows that their exospore is three-layered, with cavities in the middle layer. Preliminary study of 'trimerophytes' (Gensel, 1980) shows that the exospore is two-layered, the outer, sculptured layer separating readily from the inner one.

The exospore ornamentation of ophioglossalean spores ranges from warty through spiny (as in Marattiales) to distinctly foveolate, a more complex condition than occurs in Marattiales though some species of *Archangiopteris* show an approach to this. Psaroniaceae shows a similar range of ornamentation to extant Marattiales. Our choice of outgroups for characters 71–73 therefore proved inadequate to achieve a hypothesis of polarity of the various character states of relevance. We justify our choice only weakly, on the basis of 1. intuitive hypothesis of a simple to complex transformation series (i.e. warts → short spines → long spines → branched spines → reticulate/foveolate) and 2. wider outgroup comparison with 'trimerophytes'. However, the evidence from 'trimerophytes' (Gensel, 1980) suggests that short spines are plesiomorphous, in which case the warts of some marattialean spores would be better interpreted as apomorphous (character 71).

Results and discussion

Using the method outlined on p. 226, the information in Table 2 was used to construct the cladogram shown in Fig. 23, which is summarised in skeletal form in Figs 24 and 25J. The pages which follow discuss the cladogram within the constraints of taxonomic relationships and compare it with previous classifications. The cladogram proves to be more highly resolved than these previous classifications in terms of internested taxa and enables clear definitions to be formulated of Marattiales as a whole, of the Psaroniaceae and of extant Marattiales (Marattiaceae), each of which taxa is shown to be cladistically natural. Within the Marattiaceae, except for *Christensenia* and *Danaea*, the current generic circumscriptions are not cladistically natural: *Marattia, Macroglossum, Angiopteris*, and *Archangiopteris* are all 'paraphyletic'. This reveals a need for further work on these genera. In the interim a provisional written classification is provided which incorporates some paraphyletic taxa.

Comparison of the cladogram with previous classifications

The scope of the term classification is generally limited to mean 'systems of words' (Wiley, 1981). Such classifications are here referred to as 'written classifications' or 'classifications in writing'. In our opinion diagrams such as cladograms are also classifications (Eldredge & Cracraft, 1980; Hill & Crane, 1982: 277), and may be referred to as 'diagrammatic classifications'.

An important property of diagrammatic classifications is the means they provide for comparison which overcomes the limitations traditionally imposed on written classifications by the Linnaean hierarchy. To this extent, adherence to the Linnaean hierarchy can be viewed as a weakness of classifications in writing (but see p. 278). Diagrammatic classifications also facilitate demonstration of the characters used to define taxa, which is not economically possible (nor desirable) with written classifications.

The distinction between written and diagrammatic classfications is not, however, absolute. In this paper our results on Marattiales are presented in four versions of classification. There is the entirely diagrammatic cladogram in Figs 23 and 24. Figure 23 shows the synapomorphies and homoplasies (a cladogram sensu stricto), Fig. 24 is without them (a cladogram sensu lato). A classification entirely in writing is given on p. 278 and a classification intermediate between it and a cladogram (an annotated cladogram) is given in Fig. 25J. This figure shows the taxa (lettered U–Z) that most directly represent the sequence of internested taxa of the diagrammatic classification. In principle, these taxa could all be named (as for taxon U, Marattiales and V, Marattiaceae), and to the extent that they are lettered the classification may be regarded as being partly in written form. We do not, however, formally name the taxa (other than for taxa U, V, and X) since to do so would merely clutter the literature with excess words (Harris, 1964). The main importance of these taxa is their internested relations and not their names, though clearly some names and letters are needed for discussion. It is a matter of balance.

Figure 25J may be compared with nine previous classifications of Marattiales in the literature, which are represented diagrammatically in Fig. 25A–I to facilitate comparison. (Taxon U of Fig. 25J is disregarded for this purpose since none of the previous classifications includes reference to Psaroniaceae). Comparison shows a) That the previous classifications are very varied, b) The classification favoured by more authors than any other, Fig. 25A, is the least resolved in terms of internested taxa. Thus, although the least controversial classification, it is also the least informative in these terms. It is in fact totally uninformative. c) The cladogram is considerably more resolved than any of the previous classifications. Excluding taxon U, Fig. 25J has five internested taxa (ranks), whilst the maximum in the other classifications is two ranks (Fig. 25B–I), with the minimum of zero internesting, i.e. one rank only, in Fig. 25A. d) The classifications nearest to the cladogram are those of M. D. Crane (Fig. 25H; 1973) and Devi (Fig. 25I; 1981).

The previous classifications vary mainly because they do not fully resolve taxon W of Fig. 25J separately from V, nor X from W. *Marattia* is the 'joker', resolved with difficulty amongst these schemes as well as in ours. It appears in more different positions relative to other taxa than any of the other genera. Grouping X remains essentially constant throughout except for Pichi Sermolli's (1957, 1977) scheme (Fig. 25F), which reflects the erroneous view that *Protomarattia* resembles *Marattia* more closely than *Archangiopteris*.

We do not wish to imply that when cladograms of Marattiales are produced by different authors they will prove to lack variety. Results will vary according to the scope and number both of terminal taxa and of characters utilized, and depending on the exact method and polarities chosen. Some of the taxa U–Z are based on few synapomorphies and may well prove sensitive to change. This is another reason for our reluctance to formally name some of these taxa. Nonetheless, we would be surprised if cladograms produced in the future (assuming they are based on a comparably wide range of characters) prove to vary as widely as the previous classifications in terms of the sequence of internesting of the taxa.

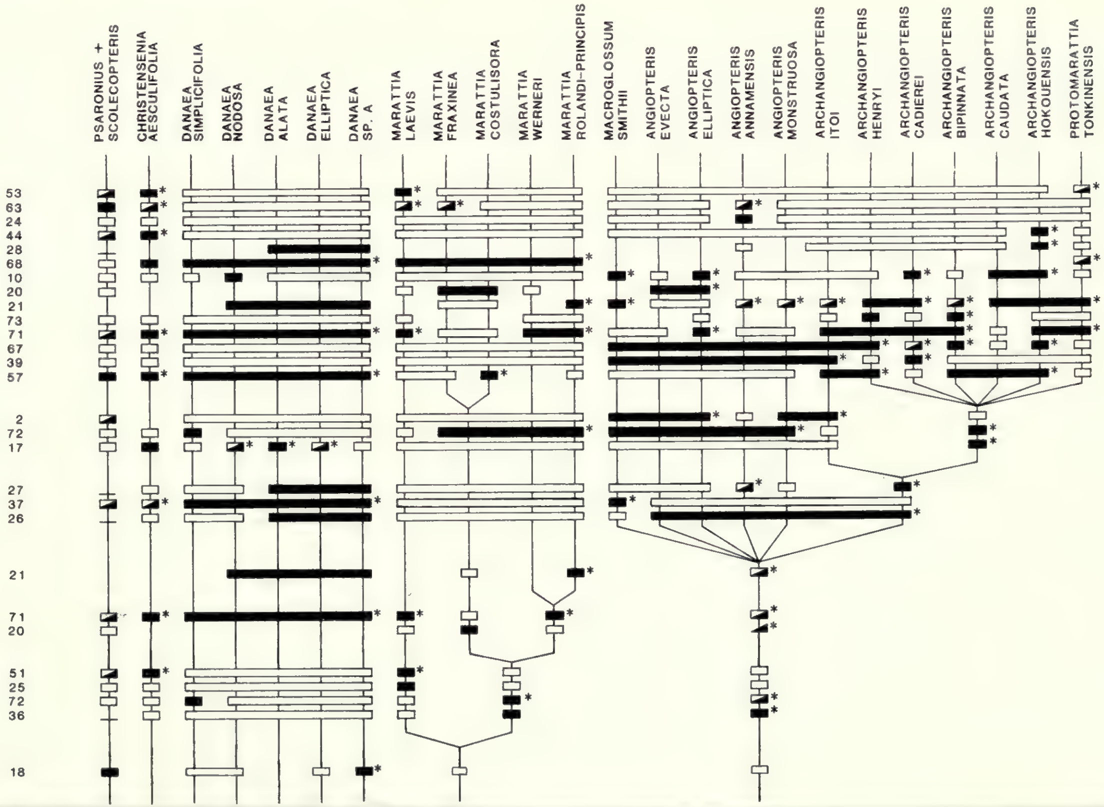
Two criticisms should be levelled at our comparisons. Firstly, the authors of the previous classifications did not intend them to be presented diagrammatically in class inclusion terms as if they were cladograms. Secondly, and more importantly, since the previous classifications are tied to the Linnaean hierarchy at the ranks of order and family, it is unjustified to expect more than two internested taxa to have resulted from them. We would accept this criticism, and merely state that we know of no other useful grounds for comparison: to refrain from such comparison for these reasons would clearly lead nowhere, whereas to make the comparison leads somewhere. Indeed, regardless of these considerations there are two important conclusions. Firstly, the cladogram unequivocally achieves a considerably greater resolution of internested relations of the taxa than the previous, more traditional classifications. Secondly, this greater resolution is a result of freedom from the restricted internesting of ranks maintained by conventional usage of the Linnaean hierarchy. This greater resolution of class inclusion

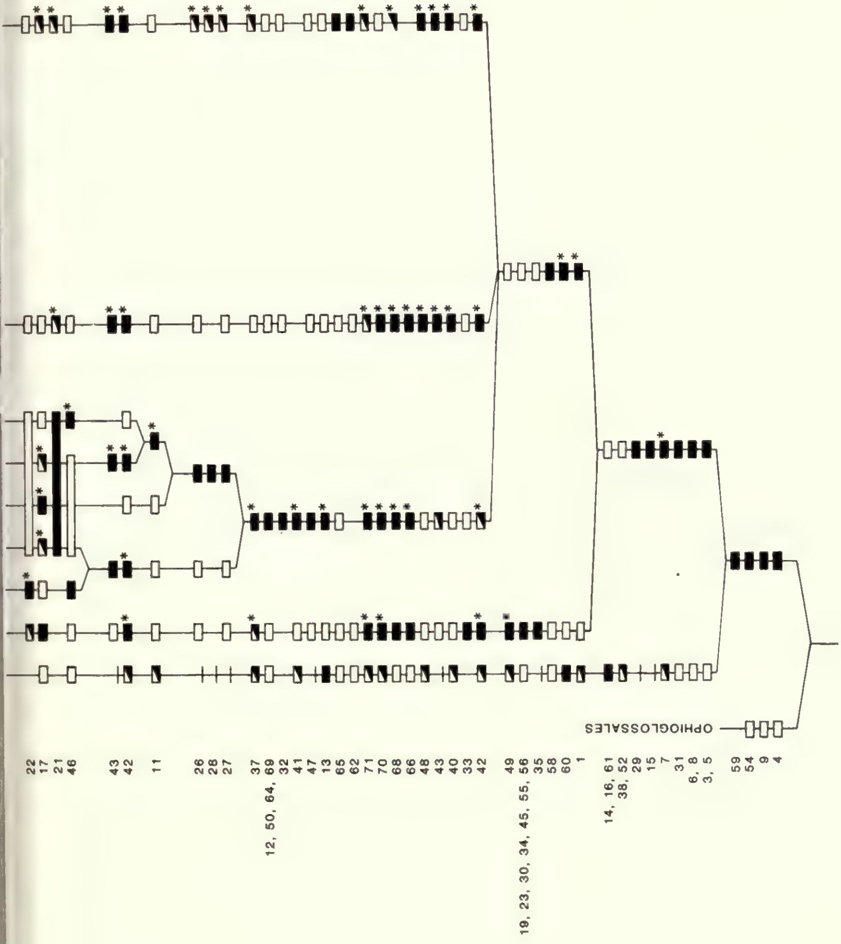
Table 2 Data matrix for the two-state characters of Marattiales listed in the text. Plesiomorphous state shown as −, relatively apomorphous as +. Those marked −/+ show both plesiomorphous and apomorphous states in the same taxon. / indicates a character is not applicable. Parentheses are used where data are more or less conjectural, blanks are left where prediction seemed ill-advisable; both symbols indicate where further observation is needed.

Character	Ophioglossales	*Psaronius* + *Scolecopteris*	*Christensenia aesculifolia*	*Danaea elliptica*	*Danaea nodosa*	*Danaea simplicifolia*	*Danaea alata*	*Danaea* sp. A.	*Marattia fraxinea*	*Marattia rolandi-principis*	*Marattia werneri*	*Marattia costulisora*	*Marattia laevis*	*Angiopteris evecta*	*Angiopteris annamensis*	*Angiopteris elliptica*	*Angiopteris monstruosa*	*Macroglossum smithii*	*Archangiopteris henryi*	*Archangiopteris itoi*	*Archangiopteris cadierei*	*Archangiopteris bipinnata*	*Archangiopteris caudata*	*Archangiopteris hokouensis*	*Protomarattia tonkinensis*	'*Radstockia*' *kidstonii* Taylor	*Qasimia schyfsmae* (Lemoigne) Hill, Wagner & El-Khayal	*Angiopteris blackii* Van Konijnenburg-Van Cittert
1	−/+	−/+	−	(+)	+	(+)	+	(+)	+	(+)	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)			
2	−	−/+	/	−	−	−	−	−	−	−	(−)	(−)	(−)	+	−	(+)	(+)	(+)	−	(+)	(−)	(−)	(−)	(−)	−			
3	/	−	+	+	+	+	+	+	+	+	(+)	(+)	(+)	+	+	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	+			
4	−	+	+	+	(+)	+	+	(+)	(+)	(+)	(+)	(+)	+	+	(+)	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)			
5	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	(+)	+	+	(+)	(+)	+	+	+	+			
6	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−?	+?	+?
7	−	−/+	+	+	+	+	+	+	+	+	(+)	(+)	(+)	+	+	(+)	(+)	+	+	(+)	(+)	(+)	(+)	(+)	+			
8	−	−	+	+	+	+	+	+	+	+	+	(+)	+	+	(+)	+	(+)	+	+	(+)	(+)	(+)	+	+	+			
9	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
10	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	+	−	+	+	−			
11	−	−/+	−	+	−	−	−	+	−	−	(−)	(−)	(−)	−	−	(−)	(−)	−	−	(−)	(−)	(−)	(−)	(−)	−			
12	−	−	−	+	+	+	+	+	−	−	−	(−)	−	−	(−)	−	(−)	−	(−)	(−)	(−)	(−)	−	−	−			
13	−	+	−	+	+	+	+	+	−	−	−	(−)	−	−	(−)	−	(−)	−	(−)	(−)	(−)	(−)	−	−	−			
14	−	+	−	−	(−)	−	−	−	−	−	(−)	(−)	−	−	(−)	(−)	(−)	−	−	(−)	(−)	(−)	(−)	(−)	(−)			
15	/		+	+	+	+	+	+	(+)	(+)	+	(+)	+	+	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)	(+)			
16	−	+	−	−	−	−	−	−	−	−	−	(−)	−	−	(−)	−	(−)	−	−	(−)	(−)	−	−	−	−			
17	−/+	−	+	−/+	−/+	−	+	−	−	−	−	(−)	−	−	(−)	−	(−)	−	+	−	(+)	(+)	(+)	(+)	+			
18	−	+	/	−	−	−	/	+	−	−	−	(−)	−	−	(−)	−	(−)	−	/	−	(/)	(/)	(/)	(/)	/			
19	−/+	−	+	−	−	−	−	−	−	−	−	(−)	−	−	(−)	−	(−)	−	−	(−)	(−)	(−)	(−)	(−)	−			
20	−/+	−	/	/	/	/	/	/	+	/	−	+	−	+	/	+	/	/	/	/	/	/	/	/	/	−	+	+?
21	−/+	/	/	+	+	/	+	+	−	+	/	−	/	−	−/+	−	−/+	+	+	−/+	+	−/+	+	+	+	/	−	−?
22	−/+	/	−/+	−	−	+	−	−	/	−	/	/	/	/	/	/	/	−	−	−	−	/	−	−	−	/	/	/

23	−/+	−	+	−	−	/	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
24	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−			
25	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−			
26	−		−	(+)	(−)	(−)	(+)	(+)	(−)	(−)	(−)	(−)	(−)	+	(+)	(+)	(+)	−	(+)	(+)	(+)	(+)	(+)	(+)	(+)			
27	−		−	+	−	−	+	+	−	−	−	−	−	−	−/+	−	(−)	−	+	+	(+)	+	+	+	+			
28	/		/	+	/	/	+	+	/	/	/	(/)	/	/	−	/	(/)	/	−	−	−	−	−	+	−			
29	−/+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
30	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−	
31	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		−	
32	/	/	/	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−	
33	/	/	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−	
34	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−	
35	−		+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−	
36	−		−	−	−	−	−	−	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+			
37	−/+	−/+	−/+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	+	−
38	−	−/+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
39	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	−	+	+	−	−	−	−	−	−/+	−
40	/	−/+	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
41	/	−/+	−	+	+	+	+	+	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/			
42	/	−/+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
43	/	?	−	+	+	+	/	/	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
44	−/+	−/+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−			
45	−/+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
46	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
47	+		−	+	+	+	+	(+)	−	−	(−)	(−)	−	−	−	−	(−)	−	(−)	(−)	(−)	(−)	(−)	−	(−)		+	−
48	/	−/+	−	−	−	−	−	(−)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
49	−	−/+	+	−	−	−	−	(−)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−			
50	−	−	−	+	+	+	+	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−
51	/	−/+	+	−	−	−	−	(−)	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−			
52	/	−/+	−	−	−	−	−	(−)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−			
53	−	−/+	+	−	−	−	−	(−)	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−/+	−	−	−
54	−	+	+	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
55	/	−	+	−	−	−	−	(−)	−	−	/	−	/	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
56	/	−	+	−	−	−	−	(−)	−	−	/	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
57	/	+	+	+	+	+	+	(+)	−	−	/	+	−	−	−	−	−	−	+	+	−	+	+	+	−	−	+	−/+
58	/	−	−	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
59	/	+	+	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−
60	−	+	−	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
61	−	+	−	−	−	−	−	(−)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−?	−
62	−	−	−	/	/	/	/	(/)	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+		+	−
63	/	+	−/+	−	−	−	−	(−)	−/+	−	−	−	−/+	−	−/+	−	−	−	−	−	−	−	−	−	−	−	−	−/+
64	/	−	−	+	+	+	+	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
65	/	−	−	−	−	−	−	(−)	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+
66	/	−	+	+	+	+	+	(+)	+	+	+	+	+	/	/	/	/	/	/	/	/	/	/	/	/	+	+	/
67	/	−	−	−	−	−	−	(−)	−	−	−	−	−	+	+	+	+	+	+	+	−/+	+	−	+	−	−	−	+
68	/	−	+	+	+	+	+	(+)	+	+	+	+	+	/	/	/	/	/	/	/	/	/	/	/	−/+	+	+	/
69	−	−	−	+	+	+	+	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−		−?	−
70	−	−/+	+	+	+	+	+	(+)	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
71	−/+	−/+	+	+	+	+	+	(+)	−	+	+	−	+	−	−	+	−	−	+	+	+	+	−	+	+	/	−	−
72	−/+	−	−	−	−	+	−	(−)	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	/	−	+
73	−	−	−	−	−	−	−	(−)	/	−	−	/	−	/	/	−	/	/	+	−	−	+	/	−	−	/	/	/

Fig. 23 Cladogram based on Table 2, showing plesiomorphous character states ☐, apomorphous character states ■. Character states marked ◪ show both plesiomorphous and apomorphous states in the same taxon. ◢ is used where a character is not applicable to some species, but the apomorphous state of the character applies to others. — indicates no data; blanks are left where characters are not applicable. For practical reasons in drawing up the cladogram, characters 17, 20, 26, 27, 28, 37, 42, 43, 68 and 72 are represented twice, characters 21 and 71 three times. * shows homoplasies. See p. 226 for method of producing this cladogram.


PSARONIUS + SCOLECOPTERIS
CHRISTENSENIA AESCULIFOLIA
DANAEA SIMPLICIFOLIA
DANAEA NODOSA
DANAEA ALATA
DANAEA ELLIPTICA
DANAEA SP. A
MARATTIA LAEVIS
MARATTIA FRAXINEA
MARATTIA COSTULISORA
MARATTIA WERNERI
MARATTIA ROLANDI-PRINCIPIS
MACROGLOSSUM SMITHII
ANGIOPTERIS EVECTA
ANGIOPTERIS ELLIPTICA
ANGIOPTERIS ANNAMENSIS
ANGIOPTERIS MONSTRUOSA
ARCHANGIOPTERIS ITOI
ARCHANGIOPTERIS HENRYI
ARCHANGIOPTERIS CADIEREI
ARCHANGIOPTERIS BIPINNATA
ARCHANGIOPTERIS CAUDATA
ARCHANGIOPTERIS HOKOUENSIS
PROTOMARATTIA TONKINENSIS
53
63
24
44
28
68
10
20
21
73
71
67
39
57
2
72
17
27
37
26
21
71
20
51
25
72
36
18


OPHIOGLOSSALES
12, 50, 64, 69
19, 23, 30, 34, 45, 55, 56
14, 16, 61
38, 52
6, 8
3, 5

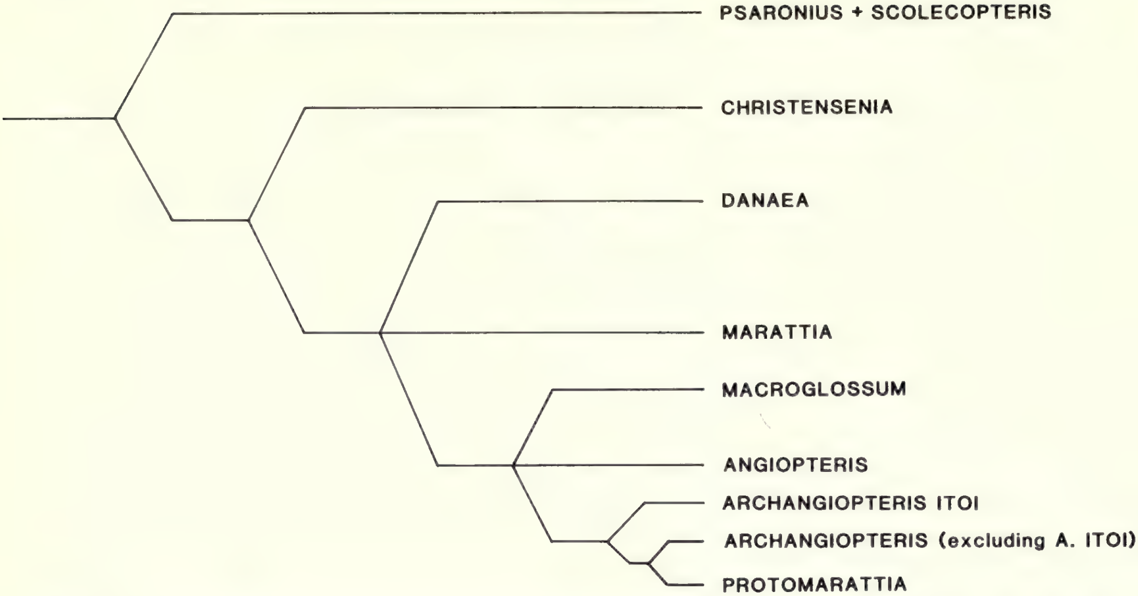


Fig. 24 Skeletal cladogram of extant genera and the out-group *Psaronius* + *Scolecopteris*. Fig. 23 gives the cladogram in detail.

relationships is, both logically and (with very few exceptions) empirically, a general property of cladograms and is of special interest in an evolutionary context (p. 278). Viewed in this light cladistics represents something of a liberation of traditional perceptions of taxonomic relationship. Cladistics might also be considered to have liberated taxonomists from the perceived need (e.g. Wiley, 1981) to view classification as necessarily always having to be performed and discussed using words alone (see also Eldredge & Cracraft, 1980). In terms of communicating taxonomic relationships an annotated diagram, as in Fig. 25J, is both explicit and informative.

Definition and relationships of the internested taxa

Before proposing a written classification of Marattiales (p. 278) we need to concentrate on the characters that define the internested taxa U–Z referred to above, and to consider briefly the status of the terminal taxa, i.e. *Psaronius* + *Scolecopteris* and the extant genera.

In his monograph on *Scolecopteris*, Millay (1979) discusses the definition of Marattiales (taxon U of Fig. 25J) and its relation to *Psaronius* + *Scolecopteris* (which as in this paper was included within Marattiales in the family Psaroniaceae). Millay characterises Marattiales as a whole on the basis of three characters: (*a*) the 'close association or fusion' of the sporangia into synangia; (*b*) their complex stelar anatomy 'involving the production of one or more internal stelar cycles'; and (*c*) the possession of polyarch roots. Although all characteristic of Marattiales, two of these characters cannot be considered synapomorphies and, therefore, as cladistically diagnostic. Considering character *a*, structures that have been termed synangia occur also in *Ophioglossum*, though they are very different anatomically and in developmental origin from those of Marattiales and may therefore be dismissed. Our only disagreement is in fact with Millay's description of this character rather than with its substance. There can be no doubt that the mature sori of the marattialean genera *Angiopteris*, *Archangiopteris*, and *Macroglossum* are, other than occasional abnormalities, entirely free-sporangiate. In terms of objective observation of the mature semaphoronts (Hennig, 1966), to term such structures synangia is inappropriate (but see p. 289 for further discussion in an evolutionary context). Nonetheless, Millay appropriately draws attention to the close packing of the sporangia in marattialean sori, in a manner which very closely resembles that of the spore bearing loculi of the synangiate genera such as *Marattia*. The evidence for homology of the sorus with the synangium within the Marattiales in this and other characters is very strong, and is supported by the observation that the attitude of the pre-dehiscent mature sporangia is uniformly notably erect in life. No other group of living ferns shows such close packing of the sporangia in the sorus. Thus we retain Millay's character *a* as a synapomorphy for the Marattiales though described somewhat differently (character 59).

Millay's characters *b* and *c*, however, are at best of phenetic utility at this rank and are not regarded here as synapomorphies of the order. Many other ferns, for instance species of *Thyrsopteris, Saccoloma, Dennstaedtia* and *Pteris* may also have complex stelar anatomy (Ogura, 1972). Whilst these reasonably may be regarded as homoplasious occurrences, *Christensenia* and certain species of *Psaronius* appear to have a solenostele. Thus on an objective assessment this character as stated by Millay cannot be considered a synapomorphy, though it is near to being one (see discussion of character 1). Character *c*, polyarch roots, is recorded in Hymenophyllaceae, Gleicheniaceae, and in the out-group Ophioglossales (Ogura, 1972) and this too is therefore rejected here. Some Marattiales have a greater extent of polyarchy than these other occurrences but this is not a universal character for the order.

Apart from character 59, only two others appear exclusively to unite the extant Marattiales with Psaroniaceae as Marattiales sensu lato (taxon U of Fig. 25J). These are characters 4, the endarch protophloem, and 9, the occurrence of mucilage canals in the frond axes.

Definition of the extant Marattiales, i.e. 'Marattiaceae' in the sense used here (taxon V of Fig. 25J) is based on six synapomorphies: character 3, meristeles as seen in T.S. of the adult stem in cycles not clearly distinguishable from a helix; 5, occurrence of paired stipules at the base of the frond stipe; 6, occurrence of pulvini in the frond; 8, occurrence of mucilage canals in the root as well as in other organs; 15, occurrence of multicellular root hairs; 31, strongly cyclocytic stomata. All of these are vegetative characters.

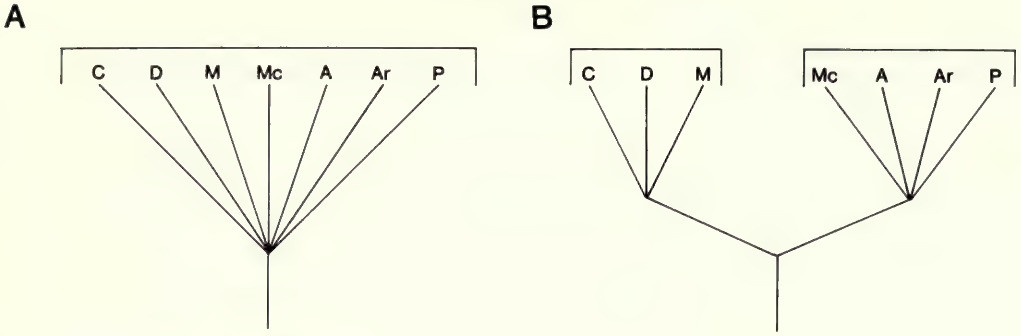
Character 15 may also have occurred in *Psaronius* but is unlikely to have been preserved. Although this is also a possible explanation for characters 5 and 6 the relevant organs of the fossils are in fact known and show no evidence of pulvini or stipules. Character 29 is shared with *Helminthostachys* and is therefore not regarded as a synapomorphy of Marattiaceae.

Within Marattiaceae the internested sub-groups are resolved by few characters. The group including all extant genera except *Christensenia* (taxon W in Fig. 25) appears to be defined by two characters: 58, elongate symmetry of the sorus; 60, lateral (and in *Danaea* ventral) walls of sporangium, or of septa between locules of synangium, composed of elongate cells. However, 60 is shared (as an apparant homoplasy) with *Scolecopteris*, and 58, though not shared with *Scolecopteris*, is shared with the fossil genera *Eoangiopteris* and *Millaya*, which may be closely related to *Scolecopteris*.

When evaluated against the six characters that set all living Marattiales apart from *Psaronius* + *Scolecopteris* and the at least three (14, 16, 61) that set *Psaronius* + *Scolecopteris* apart from all living genera, these two characters (58, 60) appear to be best assessed provisionally as homoplasious with Psaroniaceae, and thus as reasonably clear synapomorphies of group W. Further study, however, may show this to be mistaken.

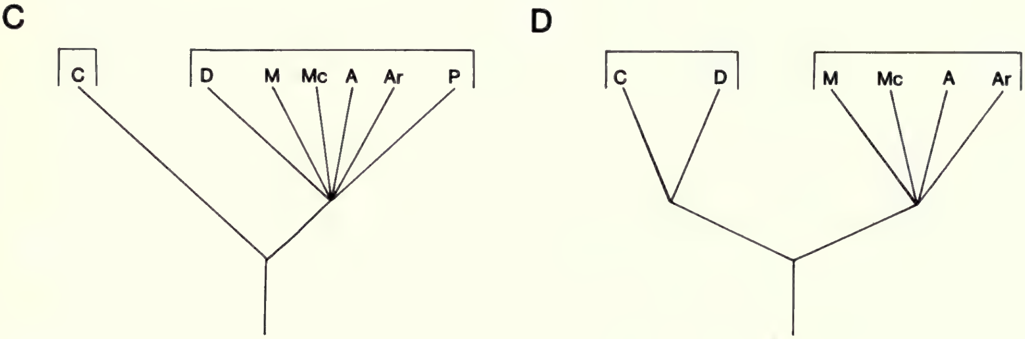
Within the internested sub-groups of taxon W, cladistic definition is generally weak in terms of numbers of characters. The abundant homoplasies create considerable 'noise'. Figures 23, 24, and 25J show that *Marattia* can be resolved only at a trichotomy, which includes also the taxa a) *Danaea* and b) *Macroglossum* + *Angiopteris* + *Archangiopteris* + *Protomarattia*. This latter group (X in Fig. 25) is defined by only two characters: 62, the occurrence of a patch of more or less thick-walled isodiametric cells at the apex of the sporangium or synangial locule; and 65, ventral walls of sporangia laterally free. (Character 62 may be evident to some extent in *Marattia*, and in a few species of *Angiopteris* is only weakly developed.) Character 65 is a clear one, at any rate as viewed in an evolutionary context (p. 289), and has long been used to discriminate these genera as a sub-group (Angiopteridaceae of some authors).

Within this grouping, a sub-group of *Archangiopteris* + *Protomarattia* (group Y in Fig. 25J) is defined by character 27, stipe of adult frond with a pulvinus a short distance proximally to the laminate region. A final sub-group (Z) of *Archangiopteris* (excluding *A. itoi*) + *Protomarattia* is



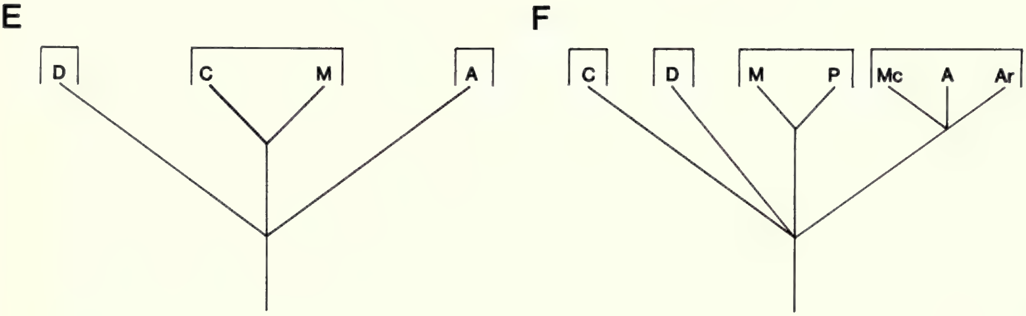
Hooker & Baker 1874
Christensen 1905/6
Alderwerelt 1908
Copeland 1947
Crabbe, Jermy & Mickel 1975
Walker pers. com. 1983

Christensen 1938



Campbell 1940

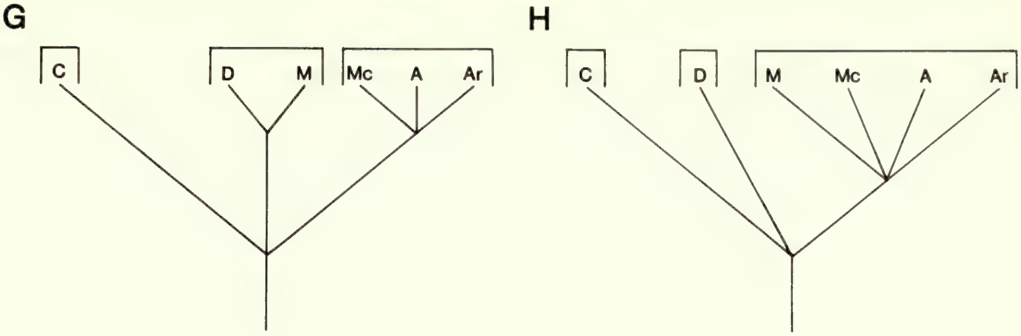
Copeland 1947 text
Bierhorst 1971



Campbell 1895

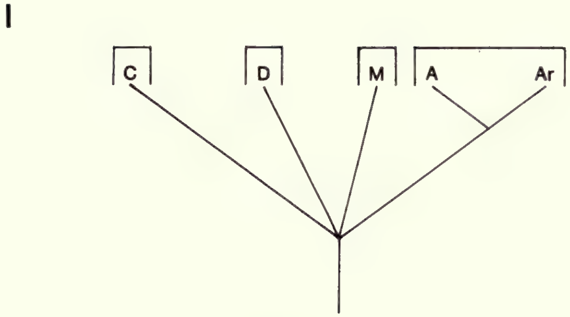
Pichi Sermolli 1957,1977

Fig. 25 **A–I**: The different family classifications within the extant Marattiales proposed by earlier workers and expressed as branching diagrams. **J**: The family classification proposed here, including *Psaronius* + *Scolecopteris*. The horizontal parentheses represent cladistic taxa U to Z. Abbreviations used for terminal taxa: C, *Christensenia*; D, *Danaea*; M, *Marattia*; A, *Angiopteris*; Mc, *Macroglossum*; Ar, *Archangiopteris*; P, *Protomarattia*; Ps, *Psaronius*; S, *Scolecopteris*.

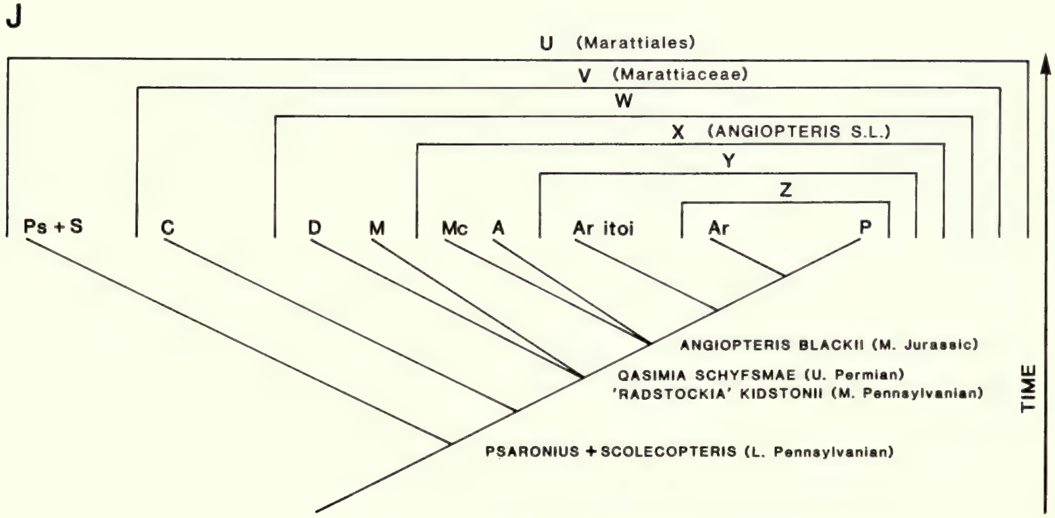

G
C
D
M
Mc
A
Ar
H
C
D
M
Mc
A
Ar

Bobrov 1973

Copeland 1947 text
Crane 1973



Devi 1981


J
U (Marattiales)
V (Marattiaceae)
W
X (ANGIOPTERIS S.L.)
Y
Z
Ps + S
C
D
M
Mc
A
Ar itoi
Ar
P
ANGIOPTERIS BLACKII (M. Jurassic)
QASIMIA SCHYFSMAE (U. Permian)
'RADSTOCKIA' KIDSTONII (M. Pennsylvanian)
PSARONIUS + SCOLECOPTERIS (L. Pennsylvanian)
TIME

defined by character 17, adult stem creeping. Sub-group Z is also defined by character 72, but this is so noisily homoplasious as to be in our view almost worthless.

Identity of Psaronius + Scolecopteris

Amongst the characters included in Fig. 23, three appear to be unique to *Psaronius* + *Scolecopteris* (14, 16, 61), with no exact counterpart amongst the extant genera. Millay (1979) gives other characters that are also unique, though to some species of *Scolecopteris* only, such as the occurrence of hairs on the synangia and of fibre-like cells in the lateral extensions of the lamina. A few characters in Fig. 23, such as 13 and 60, act as unique for Psaroniaceae in the cladogram but are nonetheless shared as homoplasies with some of the extant genera. In view of the heterogeneity of *Scolecopteris* and *Psaronius* it is possible that further study (Millay, Lesnikowska and Mickle, work in progress) may show *Psaronius* + *Scolecopteris* to be a grade assemblage.

Danaea sp. A (Figs 2, 3, 4A, B) is of special interest in showing some approach, although remote, to the tree-fern growth habit of *Psaronius*. It has an erect slender stem with elongate internodes, and thus is tree-like though the stem is less than 50 cm tall and, therefore, tiny compared to most species of *Psaronius*. The stem, as in other genera, produces roots aerially and sparsely. They are unlike the numerous roots connected by parenchymatous tissue in the external mantle of *Psaronius*. Characters shared with *Psaronius* are the occurrence of well-marked hypodermal sclerenchyma in the stem cortex and the passage of the roots initially downwards through the cortex prior to emerging (Fig. 4A). The layer of sclerenchyma is also weakly developed in other specimens of *Danaea* (see discussion of character 11, p. 240). Of these only *D. moritziana* (*A. H. G. Alston* 8539, Colombia [BM]) has elongate internodes, but its rhizome is creeping, not erect.

Definition of genera of extant Marattiales (Marattiaceae)

The 23 species selected as terminal taxa for the cladogram were chosen to represent the range of variation within the genera as currently circumscribed. This was preferred to the typological approach that has tended to characterise previous work on this group (and whereby a cladogram could more readily have been resolved). The selection partly reflects our preconception that some of the genera are not clearly defined as currently circumscribed. The cladogram (Fig. 23) supports this view for *Marattia, Macroglossum, Angiopteris,* and *Archangiopteris*, all of which are paraphyletic. None of these taxa has a single uniquely defining character apart from a few that are homoplasious with such closely related species that we consider them weak for definitional purposes (e.g. characters 10 and 21 of *Macroglossum*). *Danaea* and *Christensenia*, in contrast, are each uniquely defined by several characters. *Christensenia* is defined by ten (17, 19, 23, 30, 33, 34, 35, 45, 55, 56), of which character 17 is a homoplasy with some species of *Danaea* and with taxon Z, and *Danaea* by eight (12, 13, 32, 41, 47, 50, 64, 69), of which characters 13 and 41 are shared as homoplasies with *Psaronius* + *Scolecopteris*. These genera have long been recognised as clearly distinct, particularly *Christensenia*, which approaches *Weichselia* (Stokes & Webb) Fontaine of the Matoniaceae in the number of its unique characters (*Weichselia* has 14 in comparison with its sister genus *Piazopteris* Lorch).

Of the paraphyletic genera, *Marattia* is clearly definable phenetically by having elongate synangia (a synapomorphy of taxon W) but lacking the synapomorphies of taxon X (characters 62, 65) and of *Danaea*. For practical purposes such as field identification the genus may, therefore, be worth retaining as presently circumscribed. Cladistic revision of the generic circumscription (work in progress) would result in retention of a small number of species, such as *M. laevis*, within a narrower but more distinct circumscription, with other species placed in a closer relation to species of taxon X. To the extent that Fig. 23 does not show this, the diagram is incompletely resolved and our own approach to *Marattia* has been somewhat typological. A difficulty with cladistic revision of the genus is the almost continuous graduation of fossil forms that stretches back in time to the Permian fossil *Qasimia schyfsmae* (Lemoigne) Hill, Wagner & El-Khayal and *'Radstockia' kidstonii* Taylor of the Upper Carboniferous, most of which are cladistically 'ancestral' species (Wiley, 1981; Hill & Crane, 1982; Phillips, 1984). The alternatives to retaining a paraphyletic genus for these are (*a*) a considerable increase in the number of monotypic genera (a logical outcome of Wiley's convention 8, e.g. Bolick, 1985); or (*b*) a definition of *Angiopteris* so considerably widened as to defy practicality (another outcome of convention 8, see Phillips, 1984: 263–4). These alternatives may also apply to the extant species other than the few that could be retained within a narrower circumscription of '*Marattia*'. In either event the resulting position is distinctly counter-intuitive in terms of practical utility. It is possible under these circumstances that the most practical solution for purposes of nomenclature may be retention of *Marattia* as currently circumscribed.

These considerations underscore the view that cladistics is primarily a tool for discriminating relationships, and which are best expressed diagrammatically. In our view cladistics is of outstanding value for circumscribing taxa (both in diagrammatic and written classification) above generic rank. At generic and particularly at species rank, however, cladistics has certain limits and (other than on a non-biological worldview) can no more provide a universally valid system of classification (for species), or a universally practical one (for genera) at those ranks than any other method of classification does (cf. Wiley, 1981 and Funk, 1985). This is a direct consequence of a) Wiley's evolutionary species concept, b) the peculiar status of the genus category as a nomenclaturally obligatory higher rank for species, and c) the fact that cladograms are not designed to represent ancestor-descendant relations of species. Items a) and c) reduce to perception of evolutionary species as 'individuals' that participate in processes of change (Wiley, 1981), such that universally valid definition of species is unlikely to be possible in terms of characters alone (Hull, 1979, 1984). As Ghiselin (1980: 84) comments, 'There are no (scientific) laws for individuals . . . There are only laws for classes of individuals' (such as classes of species). To that extent it seems unreasonable to expect any one system of character classification to be universally of use for defining species (see also Hill & Crane, 1982). All such systems are of considerable value as heuristic devices since they provide a ready means of rendering species recognition operational (Mishler & Donoghue, 1982), but the only ultimate criterion, however difficult it may be to render operational, is to discriminate species boundaries in terms of process, i.e. in terms of ecological or other modes of reproductive isolation (Hull, 1965)[4]. We emphasise that there are no difficulties regarding genera viewed as classes of species, i.e. in terms of diagrammatic cladistic classification or annotated diagrammatic classifications. The problems with genera are practical ones, to do with written classification alone. We choose in this paper to resist the temptation to contribute towards either a gratuitous inflation of monotypic generic names (Harris, 1964; cf. Bolick, 1985) or of excessively broad generic circumscriptions. It is a matter again of balance, between nomenclature and relationships.

Compared to decisions (or indecision) about whether or not to dismember *Marattia* on a cladistic basis, a cladistically based solution for taxon X is less problematic. It is considerably less counter-intuitive to merge *Macroglossum, Angiopteris, Archangiopteris,* and *Protomarattia* together on cladistic grounds, within a broadened concept of *Angiopteris* sensu lato than it is to split *Marattia*. (Such a genus would scarcely be broader in terms of range of variation of form than *Danaea* or *Scolecopteris*.) Within *Angiopteris* s.l. (= taxon X) two sections, one of which is paraphyletic, may be discriminated on cladistic grounds (subject to further work), or seven sections may be recognised on phenetic grounds, as indicated below in the provisional written classification.

The notion of a broader circumscription of *Angiopteris* receives additional support from our work on intermediate forms linking the genera of taxon X as currently circumscribed. As indicated for characters 53 and 68 in Fig. 23, we have been able to establish that a continuum of intermediate specimens connects *Protomarattia* with *Archangiopteris*, to the extent that synonymy is justified on these grounds alone (Camus & Hill, in press). Similarly for *Macroglossum*, our work indicates that few of the 40 characters described by Raciborski (1902) and particularly by Campbell (1914*a, b*), justify it as distinct from *Angiopteris* when a wide range of species is examined (Hill & Camus, in preparation). For instance, their growth habit is similar, and ridges between the sori occur in both genera. *Macroglossum* in fact appears to be relatively plesiomorphous compared to other species of taxon X (Fig. 25) and thus may be regarded as a cladistically 'ancestral' species (Wiley, 1981: 223). *Archangiopteris itoi* appears to have a comparable relationship to other species of *Archangiopteris*.

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[4] Unfortunately such criteria are as yet completely unknown for Marattiales.

Provisional written classification of Marattiales

The earlier part of this discussion concentrated on the remarkable resolving power of cladistics and pointed out how this liberates the taxonomist from constraints on ranking imposed by traditional adherence to the Linnaean hierarchy. Despite this, considerable effort in recent years has gone into evolving a modified usage of the Linnaean hierarchy suitable for cladistics, termed an 'annoted Linnaean hierarchy'. This has enabled written cladistic classifications to be produced that violate the traditional Linnaean ranks as little as possible, whilst maintaining the capacity to retrieve the exact form of branching of the cladogram from the classification in writing. The modified hierarchy involves a number of conventions such as 'sequencing' and the use of † for fossil taxa. For a perceptive introduction to this cladistic mode of written classification the reader is referred to Eldredge & Cracraft (1980: chapter 5) and for a particularly comprehensive summary to Wiley (1981: chapter 6). The classification which follows uses six of the conventions discussed by Wiley and follows recommendation two of Phillips (1984: 270).

Order: Marattiales
  † Family: Psaroniaceae
      † Genus: *Psaronius* + *Scolecopteris*[5]
      † Other genera: not included in this study
    Family: Marattiaceae
      Genus: *Christensenia*
    The following taxa shown at this rank are all *sedis mutabilis*
      Genus: *Danaea*
      →
      Paraphyletic taxon: *Marattia incertae sedis*
      Genus: *Angiopteris* s.l. (*A. smithii* Raciborski)
        Paraphyletic section: *Angiopteris incertae sedis*
        Section: *Archangiopteris* (*A. itoi*)

(An alternative, phenetic classification of *Angiopteris* s.l. is offered for practical purposes:
  Section: *Macroglossum*
  Section: *Monstruosa*, for *Angiopteris monstruosa*
  Section: *Angiopteris*
  Section: *Annamensis*, for *Angiopteris annamensis*
  Section: *Itoi*, for *'Archangiopteris' itoi*
  Section: *Archangiopteris*
  Section: *Protomarattia*)

We emphasise that this classification is subject to change based on future work, particularly for taxa listed below the point indicated by the arrow.

II. Phylogenetic relationships (evolutionary cladistics)

Introduction

Part I of this paper has discussed Marattiales entirely from the viewpoint of character classification and in terms of taxonomic relationship. An important conclusion was that cladistics has a greater resolving power than alternative methods of classification[6]. To this extent the cladogram of Marattiales is more finely tuned than previous classifications of the group and brings its taxonomic relationships into considerably sharper focus. Though this can be regarded as a worthwhile goal in its own right, the purpose of this second part of the paper is to explore the ramifications of this resolving capacity of cladistics within a broader context than that of taxonomic relations alone[7]. The views presented are an explication of the evolutionary cladistics research programme initiated in outline by Hill (1981*a*) and touched upon by Hill & Crane (1982). The present account, however, remains introductory and provisional rather than definitive, and work is in progress aimed at developing the programme further. The main object of this paper is to apply the principles of evolutionary cladistics to detailed study of a group of organisms that provides in many respects a particularly appropriate test-case.

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[5] Linking of taxa by + is an informal designation for reconstructions of fossil plants when their organs, since they are not normally found in mutual attachment, are named separately (*Psaronius* = stem, *Scolecopteris* = fertile frond).

[6] As established in part I, this greater resolving power is in terms of internesting of taxa, i.e. in the number of ranks of groups within groups (Fig. 1C). In terms of the total number of taxa, including those that are not internested, other

Principles of evolutionary cladistics (sequence analysis)[8]

The basic ideas of evolutionary cladistics are simple. Firstly, cladograms are conjectured to represent something of interest in relative terms about evolutionary history (phylogeny). Secondly, this conjecture is evaluated by reference to pertinent evidence that is independent of the evidence used to formulate the cladogram. The pages which follow attempt to explain this more fully. No full attempt is made in this paper, however, to describe the 'hypothetico-deductive' framework of hypothesis-testing which provides the philosophical context within which the programme is conducted, nor to fully explicate all the hypotheses involved[9, 10].

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methods may resolve just as many as cladistics and sometimes may resolve more. For instance in Fig. 1, traditional taxonomy recognises three taxa, Seed Plants, gymnosperms and Angiosperms, whereas cladistics recognises only two: Seed Plants and Angiosperms. Similarly, for Marattiales some classifications have several sub-groupings, e.g. Pichi Sermolli's (represented here in Fig. 25F), which has four named families within the order. It therefore bears repeating that cladistics has greater resolving power in terms of the class inclusion relationship, i.e. in terms of internesting of taxa (of groups within groups).

[7] This should not be interpreted to imply that taxonomic relationships are somehow considered unimportant or less important than phylogenetic relationships. The two are in our view equally important.

[8] Sequence analysis is an alternative name for this research programme. 'Evolutionary cladistics' emphasises the aims and theoretical context of the programme, whilst 'sequence analysis' emphasises the practical form in which predictions and retrodictions are proposed and tested.

[9] For relevant introductions to philosophies of science the reader is referred to Wiley (1981: 15–20), Harré (1972), Hull (1974, 1979, 1983), Lakatos (1968, 1970), and Van Dongen & Vossen (1984). A comparable programme to evolutionary cladistics has also been outlined in 'inductivist' terms by Kluge (e.g. 1983, 1984: 29 (final paragraph), 33). Kluge's approach, like that of evolutionary cladistics, stresses the importance of the use of independent evidence, referring to the theoretical (evolutionary) context in terms of common genealogical cause and natural kinds. It is possible that this approach could be further developed within inductivist philosophy. In a hypothetico-deductive context, whilst Kluge's views are recognised here as an extremely important contribution, they appear mostly to be subsumed by those given in this paper.

[10] Distinction must be drawn between 'naïve' and 'sophisticated' approaches to hypothesis-testing (Lakatos, 1968, 1970; Van Dongen & Vossen, 1984). The view adopted by evolutionary cladistics is that of 'sophisticated' falsificationism and is in sharp contrast to many previous applications of hypothetico-deductive method in systematics (which almost uniformly as applied by cladists have been depressingly naïve). Hypothetico-deductive method is here visualised as applied most appropriately to broad and highly explanatory hypotheses such as 'descent of organisms has involved modification of their characters' or 'reversals have only occurred for adaptive reasons'. Applications of the method to cladistics by, for example, Nelson (1978), Gaffney (1979), and Kluge (1984: 29–32), whilst in themselves harmless have been narrow in scope and unimaginative. The harm they have done is to obscure a wider view of hypotheses, such as those involved in evolutionary cladistics, and which is, in fact, the kind of scope intended for hypothetico-deductive method by its main proponents (Popper, 1959; see also Hull, 1983). An example of naïve falsificationism is Nelson's (1969, 1978) view that stratigraphic ages of fossils are unimportant. A commonly held view is that this is because incompleteness of the fossil record can always be proposed as an ad hoc hypothesis (viewed naïvely as an insulating hypothesis) to explain away inconsistencies with a cladogram. An equally naïve view is held by those palaeontologists who have routinely used this ad hoc escape route in attempting to champion the universal supremacy of palaeontology, and against whom Nelson was rightly reacting. The main result of Nelson's views on stratigraphy, however, is unfortunately that nothing of use results! The naïve palaeontologists continue in their naïve views. Nelson continues in his and therefore dismisses the fossil record essentially as irrelevant: 'But what is it really, this fossil record? Only data in search of interpretation. All claims to the contrary . . . are so much superstition'. On any view of science as an activity that leads to progress, this statement, whilst true, is hopelessly negative in style. What is important is to seek out an appropriate mode of interpretation.

A sophisticated view, in contrast, recognises that (*a*) (for example) fossil or ecological evidence exists and, (*b*) although incomplete and imperfect, such evidence may be used positively in a programme of hypothesis-testing rather than ignored. If obtained, a 95% (for example) consistency of stratigraphy with a cladogram would be viewed

As a preamble to introducing evolutionary cladistics it is instructive to appreciate that there is no logically necessary connection between the cladogram of a group and its evolutionary history (Eldredge & Cracraft, 1980: 147–151; Patterson, 1980*a, b*). Since a cladogram is a classification scheme based entirely on characters of organisms, as established in part I of this paper, it clearly contains no information that is necessarily of historical relevance. It is a classification scheme that encompasses solely a logical notion of transformation, from more universal classes to less universal classes (Platnick, 1979).

The only problem with this logical position is that it has no necessary scientific relevance. This is because on current assessment of scientific activity, such strict applications of logical necessity have, by definition, a useful but limited role to play (Hull, 1979, 1983). Scientists (as opposed to logicians) pursue such questions as whether a cladogram may have some actual connection to observed reality, i.e. an empirical connection. If there appears to be such a connection, the result is to be considered scientifically relevant since knowledge of reality is thereby expanded. (Similar considerations apply also to Natural Selection, which has been rejected by some as 'tautologous'. If Natural Selection is shown to work, however, its logical standing is irrelevant.) The danger in accepting only a logical view of there being no necessary connection between cladograms and phylogeny (or that Natural Selection is 'tautologous') is that scientific knowledge would not even have a starting chance of being improved.

If an empirical connection does exist, however, between cladograms and phylogeny, how is it to be recognised? What does science do that logic alone precludes? Scientists who use the hypothetico-deductive approach in fact do two things that cannot be fully explained in terms of formal logic. Firstly, (*a*) they formulate a general idea (universal hypothesis) about how there may be such a connection; and secondly, (*b*) this is checked critically by reference to particular observations of perceived reality, to assess whether or not the idea is of use. That is, scientists a) conceive a universal hypothesis (an explanation), which may originate purely as a conjecture created in the imagination, and b) test it hard against reality. The driving force behind this is a genuine wish to understand reality (cf. Hull, 1984). Faulty ideas can therefore be rejected and worthwhile ones sifted out. Moreover, old hypotheses may be modified (Van Dongen & Vossen, 1984). For example, using universal hypotheses (the 'covering laws' of Hull, 1974), such as those of general evolutionary theory[11], a connection may be conjectured to occur between a

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as a quite remarkable correlation in view of the limitations of the evidence available (Van Dongen & Vossen, 1984; Lazarus & Prothero, 1984). (100% correlation would clearly be a naïve expectation under such circumstances.) Inconsistencies would nonetheless be scrutinised critically. Clearly either the cladogram or the fossil evidence may be wrong in such instances, and sound judgement is necessary. Such judgement must, however, be in terms of the several subsidiary hypotheses that inevitably colour most observations (Lakatos, 1968, 1970; Hill, 1981*b*; Lazarus & Prothero, 1984). Questions to be asked are, for instance, a) whether a cladogram is well supported as a character phylogeny by other relevant evidence in its own right, e.g. molecular data, biogeography, coevolution, b) whether stratigraphic evidence is well supported or not by other relevant evidence in its own right, e.g. whether the strata are structurally inverted as opposed to correctly sequenced, and whether zone fossils have been properly identified. Only after such questions have been examined can a reasoned and informed judgement be made as to whether the cladogram or the fossil evidence in a case of conflict is more likely to be right (Hill, 1981*b*; Lazarus & Prothero, 1984). In some cases the evidence may be such that no decision may be possible at present (Lakatos, 1970).

In logical terms, such arguments are not at all straightforward and they necessarily lead to awareness that all scientific knowledge has a more or less uncertain foundation when viewed in strictly logical ('A, or not A') terms (Eldredge & Cracraft, 1980). Despite this, and indeed because of it, the scientific approach has demonstrably led to growth of knowledge over the past few hundred years.

The basic question with naïve vs sophisticated falsificationism, then, is whether one is prepared to sacrifice all progress, because to have some progress is somewhat uncertain (e.g. Nelson's negative view of stratigraphic aspects of palaeontology), or whether one is prepared to sacrifice complete logical certainty for some progress, even if somewhat uncertain (our view). We personally prefer some progress. Popper (1959: 111) aptly remarks: 'The empirical basis of objective science has . . . nothing "absolute" about it. Science does not rest upon solid bedrock. The bold structure of its theories rises, as it were, above a swamp. It is like a building erected on piles. The piles are driven down from above into the swamp, but not down to any natural or "given" base; and if we stop driving the piles deeper, it is not because we have reached firm ground'.

[11] A distinction is made here between general evolutionary theory (involving such hypotheses as 'descent of organisms has involved modification of their characters') and special, Darwinian, theory which incorporates the notion of natural selection as a process leading to adaption of organisms to their environments. See also Van Dongen & Vossen (1984) for a comparable distinction.

cladogram of a group and its evolutionary history. Such a conjecture may be tested by reference to appropriate evidence. If found to withstand the test, the importance of such a demonstrated connection is that it would be empirical, of scientific interest and value, rather than merely a matter of logical necessity.

At its simplest and most naïvely stated, a basic phylogenetic conjecture which is a component of general evolutionary theory is to assume the existence of a time axis for a cladogram, which may thus be assumed to represent a hierarchical phylogeny (Fig. 25J). The sequence of internesting of internested taxa is thereby assumed to represent the sequence of their evolutionary origin through time. There are several ways in which such predictions may be tested. Clearly a 'test' that used exactly the same evidence (i.e. the same characters) as the cladogram would be completely circular and therefore futile. Hence there is a requirement that evidence used for testing should be in some degree independent of that used to formulate the cladogram. In practice, evidence can be of the same *type* (i.e. based on characters) but may be considered independent in terms of its theoretical (biological) context. For example, a cladogram based on morphological data may be compared with one based on DNA sequencing or other molecular evidence, which might be judged to be more directly expressive of genealogical change than morphology (see Kluge, 1983 and Van Dongen & Vossen, 1984: 41–42, for pertinent discussion and elaboration of this view). Both cladograms would be based on characters, but would represent conceptually different sets of characters. Equally, a cladogram may be based on vegetative characters and compared with one based on reproductive characters, representing the view that both sets of characters are subject to different selective pressures and that any similarity of the cladograms would be a direct reflection of 'propinquity of descent' (Van Dongen & Vossen, 1984). These, it seems to us, are worthwhile and important, but to the extent that they rely entirely on characters are relatively weak applications. The weakest, of course, is simply to add another character to a cladogram on a 'suck it and see' basis, as often characterises chemotaxonomic studies. Worthwhile applications are those such as Kluge's (1983) studies comparing morphological data with host-parasite data. Co-evolutionary studies have an added degree of independence in that the sets of organisms are different. Congruence suggests a common evolutionary history for both host and parasite (see e.g. Hennig, 1966 for discussion). See also Lauder (1981) on form vs function.

A different and considerably more independent set of tests, however, concerns information of a different type to characters, such as is provided by the stratigraphic sequence of fossils, and by ontogeny, biogeography and ecological evidence. To the extent that such criteria are independent of characters they may be considered to have considerably more power as tests and are the only criteria elaborated further in this paper (cf. Janvier, 1984: see also Lauder, 1981). Of the four criteria, stratigraphy is the only direct test of whether a cladogram represents phylogenetic history in terms of general evolutionary theory, and ecology is the only direct test of adaption (and therefore of, for example, Darwinian evolutionary theory). Ontogeny and biogeography appear to be relatively weak criteria but nonetheless have considerable interest.

It should be emphasised that in evolutionary cladistics it is the relative sequences of internesting that are compared, either with those in other cladograms (for the same type of data) or with other kinds of sequence as discussed below (for data of different type). Hence the alternative name of 'sequence analysis' for the research programme.

Argumentation for invoking a time axis

Stated more fully, the argumentation for invoking a time axis is as follows. Firstly, a very basic universal hypothesis in evolutionary theory is that evolution has produced change in organisms through time. To this may be added the equally hypothetical (though in general terms well corroborated) notion that during the course of such change the characters of related organisms have become transformed, from those widespread in distribution amongst organisms to those that have become more limited in distribution. In other words, change has occurred from a general form to particular or special. The sum of these hypotheses is that common descent of organisms has involved modification of their characters, Darwin's 'descent with modification'.

These ideas may be made operational as a result of the simple observation that a hierarchic classification of organisms, for example a cladogram, depicts such change (Eldredge & Cracraft, 1980: 152–157). Any resolved cladogram of diverse subjects by definition will show a sequential change from relatively general character distribution to relatively limited (special), from the bottom to the top of the diagram.

These conjectures provide the main argumentative basis for the assumption of a time axis in what then becomes strictly a phylogenetically interpreted cladogram. As a result, we may assume that the sequence of internested synapomorphies in such a cladogram, from its base to its apex, reflects a relative historical sequence (phylogenetic history). Such a phylogenetically interpreted cladogram is no longer to be considered a classification alone but nor is it an evolutionary tree diagram in any absolute sense, since the lines are not considered lineages and no ancestors are designated. The diagram represents only a more general notion of 'relative recency of common ancestry' (Hennig, 1966). Moreover, it should be appreciated that the sequence of internesting is one of taxa (viewed as historical entities (Wiley, 1980, 1981)), rather than a tree of actual organisms or of evolutionary species. Consequently a phylogenetically interpreted cladogram is to be considered an overtly abstract version of phylogeny, of narrowed scope compared to an evolutionary tree. Like many such systems in science where the scope is narrowed down (Feyerabend, 1978; Hull, 1983) phylogenetically interpreted cladograms have the capacity for sharply testing certain generalities of evolutionary theory, in particular those for which evidence is available, or can be rendered available, in the form of a relative sequence (such as ontogeny, biostratigraphy, ecology, and stratigraphy of fossils). The way in which such testing may be done is now introduced in detail using stratigraphy as an example.

Stratigraphy of relevant fossils

Such sequential relative evidence may be assessed by testing predictions or retrodictions derived from the universal hypotheses referred to above, together with any other hypotheses appropriate to the evidence being examined (Hull, 1983). For stratigraphy, few additional broader hypotheses of immediate note are needed other than the view that only the first stratigraphic occurrences of taxa are relevant to assessment of relative ages when using a cladogram in an evolutionary context: the relevant information is the relative times of origin of taxa, rather than observations on, for example, length of time of their duration or times of extinction. These latter provide interesting evidence for examining other general aspects of evolution (e.g. Gould & Eldredge, 1977; Raup & Sepkoski, 1982, 1984; Lewin, 1983) but which are inappropriate to evolutionary cladistics or vice versa. The scope of cladograms in an evolutionary context, although ideally suited for examining sequential evidence, is in fact too narrow to be able to deal with these other and equally challenging general aspects of phylogeny.

The particular set of predictions regarding stratigraphy (Figs 23, 25J) is to retrodict that the earliest occurrence of a species identifiable with more universal taxa, such as taxon U, identified by synapomorphies 4, 9, 54, 59, is expected to occur at a relatively earlier time than the earliest occurrence of a species assignable to narrower taxa, such as taxon V, identified by synapomorphies 3, 5, 6, 8, 15, 29, 31; and so on down the hierarchy, i.e. proceeding up the diagram. The important point is that such predictions are testable both in principle and frequently in practice, from the relative ages of first fossil occurrences in the biostratigraphic record, and that such tests are logically independent of the evidence that was used to formulate the cladogram, i.e. characters. Although clearly it is necessary to use the characters of a fossil as a vehicle, in order to identify its hierarchic position in the cladogram, this has no necessary connection to its time or space co-ordinates (which are its unique property as a testing ('basic') statement). In this regard characters function merely like the middle term in a syllogism, and like the sequence of internesting of taxa in a cladogram form a vehicle for testing a universal hypothesis. Neither the hypothesis nor characters alone are more fundamental than one another (contrast with the erroneous view of Patterson, 1981*b*: 213: 'These aspects are not independent, for composition *and age* . . . are largely dependent on the characterisation of the group' [our italics]). Presumably what is meant by this is that fossils must be correctly identified for their time co-ordinates to be of significance, a self-evident and uncontroversial view. The logically correct conclusion is that stratigraphy provides in practice a semi-independent test, which is as independent a test as can possibly be held to exist in science.

For Marattiales (taxon U in Fig. 25J) the first securely identifiable fossils are of *Psaronius* and *Scolecopteris* from Lower to Middle Pennsylvanian age rocks (Upper Carboniferous, Westphalian A). For taxon V there appears to be no satisfactory fossil occurrence, whilst for sphenopteroid forms of taxon W the earliest occurrence appears to be *'Radstockia' kidstonii* Taylor (Taylor, 1967), which in view of the work of Brousmiche (1983) requires a new generic name. It is of Middle Pennsylvanian age. For taeniopteroid forms of taxon W the earliest is *Qasimia schyfsmae* (Lemoigne) Hill, Wagner & El-Khayal (1985), from the Late Permian of Saudi Arabia. *Marattia* is first recorded satisfactorily some time later, from Triassic strata. For the succeeding taxa of the cladogram the only pertinent record is of *Angiopteris* (for taxon X): *A. blackii* Van Konijnenburg-Van Cittert (1975*b*; Hill, in press) from the Middle Jurassic of North Yorkshire, England. Certain Upper Triassic fossils from the People's Republic of China have also been named *Angiopteris* (e.g. Xu et al., 1979) but are unconvincing (Hill, in press).

Thus the relative sequence of first stratigraphic appearances of relevant marattialean fossils appears to match that of the internesting of taxa U, W, and X in the cladogram. This provides some corroboration for the notion that Marattiales have actually evolved through time, from those relatively generalised to those more specialised in form. Although such an idea has long been embraced by evolutionary discussions such as Bower's (1918[12], 1926), it has not previously been demonstrated for the Marattiales by such explicit initial separation of morphological from the stratigraphic evidence, nor in such detail. It provides a framework of study that is open to further assessment from criticism of what we have done, from further fossil discoveries and also from increasing depth of knowledge of the living and fossil members[13].

Although such testing using stratigraphy of fossils is a simple procedure, its empirical importance is very great. It provides the only direct means other than a time machine for concluding that a phylogenetically interpreted cladogram may actually represent a statement about phylogenetic history, which may be viewed as the product of evolutionary processes. Of its nature, only historical evidence can be expected to show directly that that history has occurred. To dismiss such evidence as essentially irrelevant (Patterson, 1977[14]; Nelson, 1969, 1978; Janvier, 1984) departs from common sense. In this respect, it seems that several systematists (and, less surprisingly, all creationists) have recently shown an incomplete understanding both of palaeontological evidence and the nature of science. For example, Kaplan (1984: 58), referring to Florin's work on homology of the coniferous cone scale, notes 'The fact that Florin's transitional forms appeared along a time sequence in the fossil record was really "icing on the cake" and not fundamental to his morphological conclusions'. To the extent that Florin's conclusions are phylogenetically valid (Kaplan, 1984: 56), the stratigraphic evidence is considerably more profound and direct than mere 'icing'.

As Kaplan (1984: 52) points out, homology has been used in two principal senses, either purely operationally (e.g. Patterson, 1982) or including some conception of common ancestry (descent). Patterson takes the operational view that homology equals synapomorphy and that that is the whole of the matter. We submit that stratigraphic testing provides the basis for discriminating whether or not synapomorphies may also represent homologies in terms of relative recency of common ancestry (Wiley, 1981). On the basis of the present research programme it cannot be maintained, to use Kaplan's words, that homologies have been defined in terms of the conclusion we might wish to reach. We have produced a cladogram, based on characters alone, and subsequently checked it against stratigraphy. Following Patterson, therefore, our homologies (methodological cladistic homologies) were determined operationally in terms of synapomorphy but subsequently evaluated (and in this instance corroborated) in terms of relative ages of origin, i.e. ancestry. Moreover, the stratigraphic test for Marattiales may be considered particularly independent (and to that extent a severe test), since the cladogram was initially based on morphology alone.

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[12] 'Such a conclusion, based on comparison, should whenever possible be checked by reference to the Fossil Record. Thus with a high degree of certainty that which is archaic may be distinguished from the more modern type, in respect of the character in question'.

[13] These fossils by no means exhaust the known genera of Palaeozoic and Mesozoic Marattiales, but excluding other Psaroniaceae they are the ones that may most securely be identified with the taxa in the cladogram. Many of the remaining genera are in need of thorough revision. *Danaeopsis* Heer, of Triassic age (e.g. Halle, 1921), for instance, is in some respects similar to *Archangiopteris*, though in others such as its reticulate venation near the pinnule margin it is very different from all extant genera. The venation therefore very distantly approaches that of *Christensenia*. Of potentially great interest in this regard is the material from the Permian of south China assigned by Li & Yao (1983) to the gigantopterid pteridosperms. Whether this material is rightly interpreted as seed plant vs marattialean is, in our view, an open question on the evidence presently available. If marattialean, the combination of synangia of fairly normal appearance borne on pinnate fronds with densely reticulate venation might prove to bridge the large gap between *Christensenia* and other extant genera.

[14] Patterson, 1977: 625, 'stratigraphic sequence can never be a trustworthy guide to phylogeny'.

The fossil genus *Qasimia* is of interest since it has stomata that are only more or less cyclocytic rather than strongly so. This conflicts with the synapomorphies established for Marattiaceae s.l. based on the extant taxa alone. Such increase in plesiomorphous character states in fossils compared to extant taxa is to be expected if evolution has occurred through common ancestry. In *'Radstockia' kidstonii* the sunken synangia are similar to *Danaea* but the round, trilete spores are similar to those of taxon X. In *Qasimia schyfsmae*, character 47 resembles *Danaea* whilst character 62 resembles taxon X. These characters mutually counteract any cladistic value that may be placed on them and such 'intermediate' character distributions compared to extant material are to be expected of fossils if evolution has occurred through common ancestry.

Although stratigraphy is of great importance in establishing whether or not an assumed phylogeny is one, it is also true that many extant groups have a poorly known fossil record. Clearly, stratigraphic testing can only be applied to such groups as Marattiales for which the record is reasonably fully known in terms of the cladogram. As such, groups like Marattiales occupy a critical position in providing a measure whereby those unsuitable for stratigraphic testing may be evaluated (Hull, 1965). To the extent that cladograms of Marattiales, Matoniaceae and other groups with a reasonably complete fossil record are concordant with stratigraphy it may be assumed that other cladograms of groups poorly represented or unrepresented by fossils are also likely to be phylogenetically sound. To the extent that groups like Marattiales have a reasonable fossil record, it is also important that evolutionary cladistic studies should to an extent be concentrated on such groups.

The use of relative sequences in evolutionary cladistics is an important quality that makes the programme particularly suitable for stratigraphic evidence of groups such as vascular land plants that can have a reasonably complete record but do not have a continuous fossil record. *Marattia*, for instance, is common in the Triassic to Jurassic and today but is unknown from the Tertiary and most of the Cretaceous. *Angiopteris* is only securely known from the Middle Jurassic and from today. It is also most unlikely that the times of origin given above are the earliest actual times of occurrence. But in relative terms enough is known of the times of first known occurrence for the record to be evidently suitably preserved.

The cladogram in fact resolves five points of internesting that may potentially be tested against stratigraphy. We note, however, that only for the three referred to above, U, W, and X, are relevant fossils available. This provides an indirect measure of the apparent incompleteness of the fossil record of Marattiales. It might even be considered by sceptical readers that in this wider, empirical context, the greater resolution of the cladogram vs former classifications of Marattiales is of no special merit in relation to the known fossils. (The former classifications in Fig. 25A–I do not include *Psaronius + Scolecopteris*, and therefore for comparison with Fig. 25J taxon V must be considered equivalent to U.) Allowing for this we may examine the extent to which Fig. 25A–I resolve taxon V vs W and X. Fig. 25A does not do so at all, whilst Fig. 25B could be used to test the ages of taxon W and X against that of V but only separately from one another, since the figure gives no internested relation for W and X. Neither is there such a relation in any other of the former classifications except for Fig. 25E and Fig. 25I. Of these, in Fig. 25E the sequence of internesting is different (and incongruent with stratigraphic evidence). Only Fig. 25I shows more or less comparable resolution to the cladogram, with W and X in an appropriately internested relation. It is interesting that this is the most recent classification. Indeed, this corroborates the view of Eldredge & Cracraft (1980: chapter 5) that there is an historical tendency in systematics towards increasingly cladistic discrimination of taxa. Cladistics, thereby, can speed up progress in systematics.

A consistent character of the fossil genera of Marattiales, with the exception of some species of *Scolecopteris*, is the shape of the surface cells of the wall of the sporangium. In *Angiopteris blackii, Qasimia schyfsmae, Acitheca adaensis* Mapes & Schabilion (1979*a*), and *Millaya tularosana* Mapes & Schabilion (1979*b*) the surface cells appear to be more or less uniformly elongate. This contrasts sharply with the living forms. These more or less uniformly show isodiametric cells near the apex, over about half or more of the height of the dorsal wall of the sporangium or synangial compartment, as shown by Figs 18A & B, 19 and 20, with *Christensenia* (Fig. 12) showing isodiametric cells over the whole surface. The only exception we have found is in a few specimens of *Angiopteris* excluded from this study, for instance in *A. ankolana* Vriese (*Junghuhn* 698, Sumatra (BM)), shown in Fig. 18D. Here there is merely the characteristic patch of thickened isodiametric cells at the extreme apex of the sporangium, with the cells otherwise more or less uniformly elongate over the whole wall.

Comparison amongst the extant species requires that such exceptions as *A. ankolana* are to be considered cladistically derived for this character. The evidence from the fossils listed above, however, conflicts with this. Although the number of fossils for which the character is known is fewer than that of the extant taxa, their relation to extant species may indicate that the polarity we have chosen, based on the sample of Marattiales available today, is incorrect.

Thus it may be eventually concluded, contrary to the discussion on p. 259, that the generalised marattialean sporangium fundamentally had uniformly elongate cells in the outermost surface layer of the sporangium wall, at any rate for taxon W. The occurrence of apparent specialisation of such cells in some species of *Scolecopteris* (Millay, 1979) and uniformly so in *Christensenia*, however, contradicts this alternative view, at any rate at a higher taxonomic rank than that of taxon W.

Biogeography

Evolutionary cladistic study comparable to that of stratigraphy may be accomplished with other sources of evidence independent of that used to formulate a cladogram, such as ontogeny, ecology, and biogeography, so long as the evidence is available in the form of a relative sequence. In biogeography an expectation is that genera of Marattiales, after initial geographic expansion, would be expected to show increasing provincialism in their geographic distributions with the passage of time. One of several problems with this is shared with that of evolutionary reversals in general, and is the same as one of those affecting Willis' similar (and ill-fated) age and area hypothesis (Willis, 1922, 1926): the geographic expansion need not always be initial since ranges may expand, contract, and subsequently again expand. If this is the case, fossil distributions ought to resolve the situation, though for fossil plants such distributional data are often of poor quality.

Taking extant distributions and referring to genera as currently circumscribed (Figs 26–27), *Protomarattia* has today (or had) a very limited geographic range in Vietnam, with *Archangiopteris* and *Macroglossum* over wider but separate areas (*Protomarattia* is nested within the range of *Archangiopteris*). These ranges all occur within the wider range of *Angiopteris*, and this in turn is included by that of *Marattia* which is pantropical. *Danaea* is of limited range in central and southern America whilst *Christensenia* is limited to south-east Asia. There is an interesting disjunction between the distribution of *Christensenia* and that of *Archangiopteris*, with one record of *Christensenia* from the extreme south of Thailand.

With the exception of *Christensenia* and *Danaea*, the internesting of these distributions more or less matches the pattern of internesting of the taxa in the cladogram. In relation to standard palaeogeographic reconstructions, the indications are that *Protomarattia, Archangiopteris*, and *Macroglossum* are exclusively Laurasian, and thus in vicariance biogeographic terms may be predicted to have been younger in origin than all the other genera which appear to be Pangean.

Of the relevant marattialean fossils the Psaroniaceae appears to have been pantropical in distribution. *Qasimia* and related ferns were widespread within the Cathaysian province of the Permian, extending from Saudi Arabia to China, whilst fossil *Marattia* from the Mesozoic is

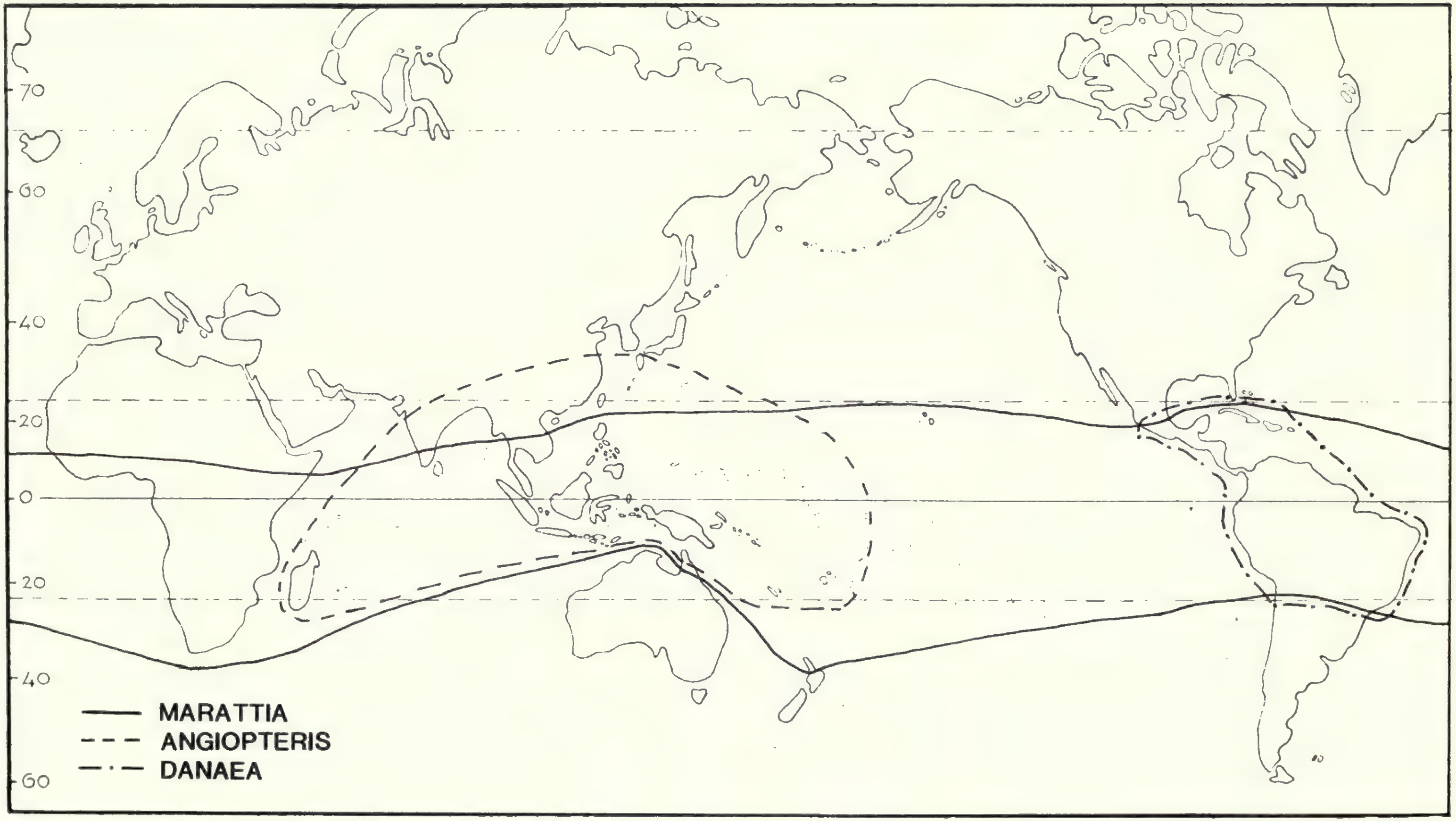
70
60
40
20
0
20
40
60
MARATTIA
ANGIOPTERIS
DANAEA

Fig. 26 Distribution of *Marattia, Angiopteris*, and *Danaea*.

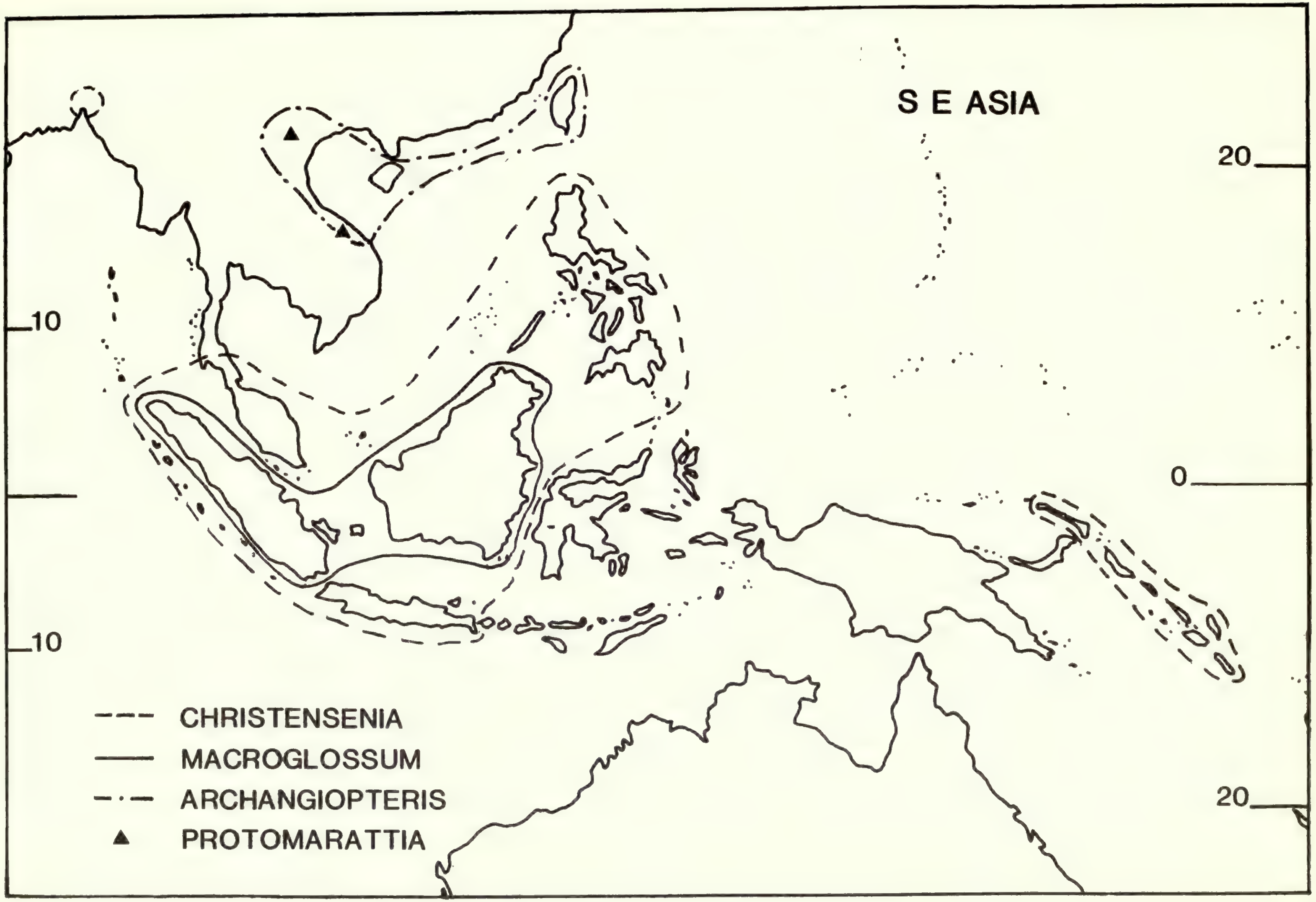
S E ASIA
20
10
0
10
20
20
0
20
--- CHRISTENSENIA
—— MACROGLOSSUM
–·– ARCHANGIOPTERIS
▲ PROTOMARATTIA

Fig. 27 Map of SE. Asia showing the distribution of *Christensenia*, *Archangiopteris*, and *Protomarattia*.

more widespread than Psaroniaceae. Fossil *Angiopteris* is known securely only from Yorkshire, England. In general, allowing for palaeoclimatic controls, this does not refute the view based on extant distributions: the U.K. record of *Angiopteris*, although unique for a fossil species of *Angiopteris*, indicates a broader distribution for the genus in the past than now.

Although the correlation of areas with the cladogram for taxon X + *Marattia* and for the taxa included within taxon X is of note, we do not consider our explanation in terms of increasing provinciality with time either particularly satisfactory or exciting, and the contradiction of the pattern by *Danaea* and *Christensenia* is disturbing. Similar considerations apply to another way of assessing cladistic and biogeography, commonly referred to as historical (or vicariance) biogeography (Nelson, 1984). That programme for biogeography, like the one outlined here, lacks a coherent theoretical context as currently formulated. The results do, however, indicate some similarities in distributions amongst different groups of organisms, though there are also contradictions which (treated naïvely like homoplasies in cladogram construction) are evidently ignored. As Nelson (1984) comments, the emerging patterns of similarity of biogeographic distributions amongst different groups of organisms require explanation.

It is difficult to enthuse over either our own or the historical biogeographic programmes on biogeography. Firstly, waxing and waning distributions in the past are well documented for instances where documentation has been possible, but are difficult to evaluate for most groups since this requires fossil evidence of a quality and completeness of availability superior to that generally available. To the extent that Recent distributions are the product of historical ones, they are not insulated from this weakness. Dispersals in plants are also well documented. Case studies could usefully be made, however, of examples of Tertiary to Recent conifers and certain Angiosperms, for which the palaeobiogeographic record is unusually complete. It is possible, in contrast to stratigraphic sequencing, that this may show biogeographic sequencing to be simply too narrow in scope to produce worthwhile results and that a more suitable device for understanding biogeography may (if only heuristically) be the evolutionary tree itself rather than phylogenetically interpreted cladograms.

Secondly, any explanation in terms of geological events (historical biogeography) or increasing provinciality (evolutionary cladistics) begs the question of how and why this is so. There is a case (in an evolutionary context) for considering ecological factors in relation to geographical space. Ecology is particularly pertinent to the problem of reversals of areas in relation to the evolutionary cladistics approach, and in turn, to reversals in a phylogenetic context.

Ontogeny

Use of ontogeny in evolutionary cladistics makes reference to the sequence of ontogenetic change undergone by tissues, organs and whole organisms during their development. It reflects the hypothesis that ontogenetic sequence in some way represents the sequence of phylogeny (Wiley, 1981). Unlike other criteria involving data of different type from that used to construct a cladogram, ontogeny is less independent and therefore is rather problematic (cf. Nelson, 1978). In practice many cladistic studies still make reference to ontogenetic sequence in order to polarise character states (e.g. Wiley, 1981). To the extent that this is done, ontogenetic sequence clearly cannot be used in any sense as a test in those studies, nor does this render testable the ontogenetic criterion itself. The approach adopted in this paper has attempted to avoid use of ontogenetic sequence data and to refer to character analysis alone. To the extent that semaphoronts (equivalent developmental stages) were compared, however, some input of ontogenetic evidence cannot (and in our view should not) be avoided. Reference to semaphoronts presupposes some knowledge of ontogenetic sequences (see discussion of characters 2, 20–23, 26–28). However, it does not necessarily presuppose the direction which an ontogenetic sequence follows. To this extent, a phylogenetically interpreted cladogram, especially when corroborated by stratigraphic evidence, may be tested by reference to the directionality of ontogenetic sequences, the expectation being that the direction (e.g. from birth to death) would be congruent with the cladogram. This is the only test that has the potential to refute ontogeny as a universally valid criterion (cf. Nelson, 1978), and so far as we are aware, is proposed here for the first time. This is not to assert that ontogeny need not under suitable circumstances refute misconceived phylogenies (e.g. Kaplan, 1984 but see also Stevens, 1980: 340–342).

In general the cladogram of Marattiales does appear to correlate with ontogeny. For instance, Fig. 25J shows clearly that the free-sporangiate forms (taxon X) are nested well within the fully synangiate ones (taxon V). This indicates in a phylogenetic context that the free-sporangiate forms probably arose from synangiate forms, and the stratigraphic evidence is clearly in support of this view. As Bierhorst (1971) points out, there is also some evidence from ontogeny to support this evolutionary view. Exactly as for the synangia of *Marattia* the sporangia of *Angiopteris* first appear in development as a linear series, with no morphological indication of the individual sporangia. In *Angiopteris* they become individualised later in development, merely through differential growth of sporangial and intersporangial regions. Bierhorst concludes 'this leads only to one interpretation: that *Angiopteris* is indeed very closely related to *Marattia*, much closer than their mature sporangiate fructifications would suggest, and that the free sporangiate condition expressed in *Angiopteris* is derived from a synangiate one.'

This is relevant to use of the term synangiate by some North American authors to describe the marattialean sorus generally (e.g. Millay, 1979; Stewart, 1983). Earlier (p. 272) we criticised the use of this term for all Marattiales since several genera at maturity have, objectively, free-sporangiate sori as in other ferns. Would that objectivity in science were so simple. Clearly on the wider evolutionary view just discussed, as opposed to a relatively narrow view based on character comparison alone, there can be no objection to Marattiales being described as fundamentally synangiate. We would still, however, disagree with them being described uniformly as synangiate (Millay, 1976, 1979), since this makes an objective hypothesis seem like fact, devoid of explanation.

Since the outgroups of Marattiales, such as Ophioglossales and 'trimerophytes', lack synangia or do not have comparable synangia, it seems reasonable to suppose that presumed evolution of free-sporangiate sori in taxon X of Marattiales represents an evolutionary reversal.

There is one clearly evident conflict with ontogenetic sequence. In general the developmental sequence of these ferns (as in most plants) proceeds from simple to complex form, as shown for frond development in Fig. 7. The cladogram, however, indicates that the phylogenetically generalised frond form of Marattiales, as evidenced by the out-groups, is three or more times pinnate, with pecopterid pinnules (as opposed to sphenopteroid or taeniopteroid in taxon W)[15]. How is this conflict of sequences regarding frond form to be resolved? Clearly either ontogeny or the cladogram may be in error. Considering the cladogram, we have already established that it is well corroborated as a statement of phylogeny by stratigraphic evidence. The possibility was also considered that frond vasculature may show evidence of loops that might indicate a formerly more divided frond, though without success[16].

Under these particular circumstances we can only conclude (reluctantly) that ontogeny is a misleading guide to phylogeny of frond form in Marattiales. Other instances in the plant kingdom also occur where phylogeny indicates progression from complex to simple, corroborated by stratigraphy, but where ontogeny proceeds from simple to complex.

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[15] It has long been held by evolutionary systematists that the taeniopteroid forms evolved from the pecopterid ones by condensation of the lamina (e.g. Mamay, 1950; Asama, 1960; Stidd, 1974), with *Christensenia* at a highly advanced stage of condensation, though no direct link with pecopterids is known. The nearest link is perhaps *Qasimia*, which retains a rounded apex to the taeniopteroid pinnules, thus providing a hint of a pecopterid pinnule outline and corresponding in this respect to Stidd's (1974) hypothetical intermediate form. Its vegetative pinnules also have an exceptionally high vein concentration. It is perhaps to be expected of plant development that no exact intermediate need ever have existed, since innovatory genetic change may have produced a leap in morphological change rather than one involving a graded series of intermediates. This is open to investigation by laboratory experiment on developmental processes, a particularly promising field of enquiry, as well as to continued search of the rocks for missing links.

[16] It seems that development of the degree of pinnation generally in extant Marattiales is unusually variable. Asama (1960) discusses an instance where low temperature is considered to have caused a typically bipinnate plant of *Angiopteris lygodifolia* to revert to the developmentally earlier once-pinnate form. Sori were produced on these less-divided fronds. We have seen a similar example amongst the Marattiales in cultivation at K, a normally tripinnate *Marattia werneri* Rosenstock plant which grew a partly bipinnate frond. Conversely, we have also seen bipinnatifid parts of the frond of the normally once-pinnate *Macroglossum smithii*, and tripinnate parts of fronds of normally twice-pinnate *Angiopteris evecta*. The cause of these aberrations in growth is not known.

Similar deviations are seen in herbarium specimens (BM, K) of species of *Danaea, Marattia* and *Angiopteris*. *Angiopteris monstruosa* Alderw. and *Archangiopteris bipinnata* Ching may be examples of such abnormalities raised to species status.

These findings are at odds with the view taken by most vertebrate zoologists and some botanists (e.g. Kaplan, 1984) that ontogenetic criteria are of paramount importance in determining homologies. There are two worthwhile possibilities. The most direct one is that the value of ontogeny as a general criterion may have been somewhat over-emphasised. An auxiliary ('ad hoc') hypothesis suggested to us by D. E. Rosen (pers. comm.) is that plants may be developmentally under different control from animals, in a manner which makes their ontogeny sometimes conflict with phylogeny. As Stevens (1980) expresses it, 'Plant ontogeny is open, rather than closed, and much of ontogeny appears to be simple compared at least to that in vertebrates'. (The hypothesis that ontogeny will always corroborate phylogeny in animals is thereby insulated from criticism.) A third view, essentially that phylogeny as understood here is irrelevant and ontogeny is all important, is so naïve and narrow that it itself is irrelevant.

Rosen's view, treated in more 'sophisticated' terms as an auxiliary hypothesis, deserves closer examination (see also Stevens, 1980). In further discussion, B. Gardiner (pers. comm.) has suggested that if plants are looked at more closely, ontogeny will be found to correlate uniformly with phylogeny. This also deserves attention (though as mentioned above, we have failed so far to find such evidence for frond form in Marattiales). Another possibility is that frond development may be extremely 'telescoped', such that relevant stages have become deleted. This might be examined by laboratory studies.

Whilst botanists, therefore, have some work to do in this regard, it does not seem unreasonable for zoologists also to reconsider instances in which ontogeny conflicts with phylogeny. Such would be pointless, however, in the absence of conjunction with the stratigraphic test, under which circumstances ontogeny would necessarily be regarded as generally superior (Nelson, 1978). For important additional discussion on the use of ontogeny in systematics see Alberch (1985).

Ecology and comparative physiology

Present knowledge of the ecology and physiology of Marattiales is so crude as to preclude ecological or physiological tests. Ecology and physiology are particularly relevant, however, in terms of adaption and, to that extent, in terms of Darwinian as opposed to general evolutionary theory. Ecological assessment may be used to examine reversals of characters, such as results in the free-sporangiate sori of taxon X, and in that sense is a test of Dollo's law which holds that evolution is irreversible (Hull, 1974). Ecology and physiology may, therefore, be used as tests to discriminate 'methodological' from 'evolutionary' synapomorphy (Hill & Crane, 1982: note 2). A pertinent example is given by Crane & Manchester (1982), in which a reversal in seed characters from wind-dispersed to a simpler form is directly interpretable in terms of adaptation for dispersal by animals.

This has some interest regarding current debate about numerical methods of cladogram construction (Churchill, Wiley & Hauser, 1984, 1985; Duncan, 1984; Farris & Kluge, 1985). It is now clear that a property of Parsimony methods is to sometimes introduce more reversals than Compatibility methods (and would also introduce more reversals than in the method of cladogram construction adopted here). It is a matter of degree, not of absolutes. Different methods, therefore, give different cladograms, particularly for highly homoplasious groups such as Marattiales. To date, the justification for one or other approach has been almost entirely axiomatic, in terms of interpretations of what Hennig wrote or in terms of a given model of evolutionary process. Few have explored the criteria considered here, which basically are designed to test the efficacy of cladograms in terms of goodness of fit with real, independent data, i.e. in terms of veracity with Nature (Wiley, 1981). It may well be that on these grounds one approach may prove to have consistently greater phylogenetic veracity than another. Equally it may be shown that approaches have variable veracity depending on the groups analysed. It is even possible that all methods may prove sufficiently uniform in terms of internested taxa (in relation to the extent of evidence available for testing) so as to dissipate the debate entirely. All we would argue is that Parsimony appears to resolve more internested sequences of taxa than alternatives, and to that extent is more falsifiable. That is, it is falsifiable in principle and, to the extent that its adherents may be prepared to admit of its falsification empirically, it is potentially falsifiable in practice (Nordal, in press). We do not mean by this, 'falsification' in the narrow character-centred sense currently used by the main proponents of Parsimony method (e.g. Farris & Kluge, 1985).

Conclusions

The aim of this part of the paper has been to take a cladogram of Marattiales, a construct based on characters alone, and to examine its veracity in terms of independent criteria: stratigraphy, ontogeny, biogeography, and (in principle) ecology, and physiology. This is done within a hypothetico-deductive context termed evolutionary cladistics, the main principles of which are given. Marattiales are unsuitable at present for ecological or physiological appraisal, but abundant evidence of good quality is available on their stratigraphy, ontogeny, and biogeography. Stratigraphy of relevant fossils shows that the cladogram has veracity in terms of phylogenetic history and, therefore, of its synapomorphies in terms of phylogenetic homology. It also indicates that a reversal has probably occurred to produce free-sporangiate sori in the genera of taxon X. In these terms the phylogenetically interpreted cladogram is regarded as a rather strongly corroborated general statement of the phylogenetic history of Marattiales. Ontogeny proves generally consistent with this view, particularly regarding the reversal to free-sporangiate forms, but conflicts with the phylogenetic hypothesis for frond form. This conflict deserves further study from several different angles. Biogeography proves consistent for taxon X + *Marattia* whereas *Christensenia* and *Danaea* are in conflict. It is considered uncertain at the present time whether the union of cladistics and biogeography has a worthwhile theoretical context.

In summary, evolutionary cladistics (sequence analysis) represents a broad view of cladistics and the uses to which cladograms may be put, a view that is aligned with (amongst others) those of Hennig (1966), Lauder (1981), Wiley (1981), Hill & Crane (1982), and Kluge (1984). It contrasts sharply with the narrower, more operationalist (Hull, 1968, 1983) and ontogeny-centred world view of such cladists as Nelson & Platnick (1981), Patterson (1982), and Janvier (1984). The overall strength of cladograms assessed in evolutionary cladistic terms, compared to phenetic or other traditional classifications, lies in the greater resolution of internesting of taxa by cladograms. Thus they are better designed for sensitive and explicit testing of certain universal hypotheses pertinent to evolution. Testing is done by reference to relative sequences of evidence that is to a greater or lesser degree independent of that used to construct the cladogram. The most important criterion in assessing a phylogenetically interpreted cladogram is empirical, i.e. its goodness of fit with such independent evidence.

Summary

1. Nine previously proposed classifications of extant marattialean ferns into families are compared. The classification showing no resolution of relationships is the one that has been favoured by most authors.

2. A cladistic method is used to produce a new classification of extant Marattiales. This is done with reference to the Palaeozoic fossil *Scolecopteris* (fertile frond) + *Psaronius* (stem) and to Ophioglossales as the main outgroups for character comparison. Further work is in progress aimed at examining alternative, numerical methods, of cladistic analysis for Marattiales.

3. The new classification proves to be more highly resolved than any of those proposed previously, having five ranks as opposed to a maximum of two in the previous classifications. The classification is represented diagrammatically by a cladogram and also in written form. Unlike previous classifications of Marattiales, the basis for the new classification is made explicit by including a data matrix and a discussion of characters, based on a detailed survey both of the literature and of the plants themselves.

4. In the new classification, Marattiales (including Psaroniaceae) is defined by three characters

that distinguish the order from its nearest extant outgroup, Ophioglossales, and from other filicopsids. The characters are 4, 9, and 59: 4, endarch protophloem of stele of stem; 9, mucilage canals in axial components of frond; 59, spore-bearing loculi of synangia, or sporangia of sori, packed closely together. Extant Marattiales (i.e. Marattiaceae) are defined by six characters, 3, 5, 6, 8, 15, 31: 3, meristeles as seen in T.S. of adult stem not in clear cycles; 5, occurrence of persistent, starch-storing stipules at the base of the rachis; 6, occurrence of pulvini in the frond; 8, occurrence of mucilage canals in the root; 15, occurrence of multicellular root hairs; 31, stomata of lamina more or less strongly cyclocytic.

5. Circumscription of marattialean genera is briefly discussed in relation to the new classification. Taxonomic judgement on such circumscription may be based in part on cladistics but to be wholly so based may present some difficulties. The following are paraphyletic in cladistic terms: *Marattia, Macroglossum, Angiopteris,* and *Archangiopteris*. *Marattia* in particular presents problems of circumscription.

6. Several characters of Marattiales are discussed or illustrated for the first time: a remarkable species of *Danaea* with an erect stem somewhat similar to that of fossil *Psaronius*, hypodermal sclerenchyma in the stem of *Danaea*, tracheids in the pedicellate placenta (receptacle) of *Marattia laevis* and *Christensenia aesculifolia*, synangial scales in *C. aesculifolia*, the well-developed placenta of some specimens of *Protomarattia*, and frond scales generally. The outermost surface layer of cells in the walls of the sporangia and synangia of Marattiales shows differentiation that may in the future prove of use in circumscribing taxa at the subgeneric level, whilst the extent of fusion of the dorsal walls of neighbouring sporangia appears to be variable and in general is of little taxonomic significance. Histochemical study of the intercellular rods on the cell walls of the spongy mesophyll (by Dr J. M. Pettitt) indicates that they are probably composed of cellulose.

7. Some persistent errors are corrected, such as the assertion (Sporne, 1975) that the walls of marattialean and ophioglossalean synangia or sporangia have stomata.

8. A programme of research termed 'evolutionary cladistics' ('sequence analysis') is outlined and applied to Marattiales as a worked example. Evolutionary cladistics assesses the veracity of cladograms in a phylogenetic context, in terms of tests based on evidence independent of that used to produce a cladogram. Its advantages are *rigour* of approach, and the greater *resolution* of internested taxa by cladograms compared to previous evolutionary systematic studies. To this extent, evolutionary cladistics is claimed to be the most explicit and sensitive device currently available for testing certain universal hypotheses of evolutionary theory. The programme nevertheless has limits. It is limited to those highly universal hypotheses that may be tested in terms of *relative* sequences, e.g. stratigraphy of first fossil occurrences of taxa, in the same sense that phylogenetically interpreted cladograms are at best a limited (though highly general) statement of the evolutionary tree. *Rigour, resolution,* and *relative*, therefore, represent the three Rs of evolutionary cladistics.

9. Using the evolutionary cladistics approach, the cladogram of Marattiales is shown to be consistent with stratigraphy of first occurrences of relevant fossils, thus demonstrating its veracity in terms of phylogenetic history. Ontogeny proves generally consistent with this view, but conflicts with the phylogenetic hypothesis for frond form. Biogeography proves consistent for most, but not all, of the genera.

10. This study is a broad overview of Marattiales concentrated on relationships and on their assessment in an evolutionary context. Whilst not formally descriptive it is preliminary to more traditional taxonomic revision. Further papers will deal with the synonymy of *Protomarattia* with *Archangiopteris*, a revision of *Archangiopteris*, the generic status of *Macroglossum* and *Archangiopteris* in relation to *Angiopteris*, and an overview of *Marattia*.

Taxa and specimens studied

The specimens listed below are those that have been studied anatomically or microscopically for the data matrix (Table 2). Other specimens examined in detail are cited where appropriate in the text and figure captions. Specimens examined only in respect to gross morphology at BM and lent by BKH, BO, E, K, KLU, L, M, MICH, NY, P, PE, TI, U, and W are not itemised. Specimens cited as K hort. number are in cultivation at the Royal Botanic Gardens, Kew. The numbers are the individual accession numbers lodged on the Living Collections Record File at K.

Christensenia aesculifolia (Blume) Maxon
A. F. Braithwaite R.S.S. 4215 and 4220, British Solomon Islands (K). *C. J. Brooks* 70S, Sumatra (BM). *C. J. Brooks* s.n., Sumatra, 1920–23 (BM). *G. E. Edaño* Philippine National Herbarium 15112, Philippines (BM). *Griffith* 1696, Assam (BM). *A. C. Jermy* 8316, Philippines (BM + pteridophyte spirit collection W.52). *A. C. Jermy* 13332, Sarawak (BM pteridophyte spirit collection S.243). *A. C. Jermy and J. M. Rankin* 14907, Sabah (BM). *W. Lobb* s.n., Java (BM). *T. G. Walker* T.13319, Sarawak (BM). *Zollinger* 1902, Java (BM). *Collector unknown*, Assam (BM).

Danaea alata Smith
including *D. wrightii* L. Underw., *D. jenmani* L. Underw. and *D. fendleri* L. Underw.
A. H. G. Alston 5114, Trinidad (BM). *Brade* 400, Costa Rica (BM). *W. E. Broadway* 6276, Trinidad (BM). *A. Fay* 844, Trinidad (BM). *A. C. Jermy* 10936 Trinidad (BM + pteridophyte spirit collection W.356). *M. Kuhn* 4681, Puerto Rico (K). *Moritz* 257, Colombia (K). *H. A. Nicholls* 194, Dominica (K). *N. Y. Sandwith* 1786, Tobago (BM). *D. Watt* 72, Jamaica (K). *C. Wright* 1066, Cuba (BM).

Danaea elliptica Smith
G. Aldridge 1834, Trinidad (BM). *W. E. Broadway* s.n., Trinidad, April 1 1927 (BM). *A. Fendler* 28, Trinidad (BM). *A. Hombersley* 354, Trinidad (BM). *A. C. Jermy* 10864, Trinidad (BM pteridophyte spirit collection W.354). *J. McCallum* 27, Trinidad (BM). *J. Miers* 260, Brasil (BM). *R. Spruce* s.n., Brasil, Dec.-Mart. 1850–51 (E). *T. G. Walker* T.10459, Trinidad (BM). *C. Whitefoord* 1215, Belize (BM).

Danaea nodosa (L.) Smith
A. Fendler 28, Trinidad (BM). *E. Hassler* 10289a, Paraguay (BM). *A. Hombersley* 240, Trinidad (BM). *Lambert* s.n., St. Vincent, 1834 (BM). *P. R. Reitz* 5.159, Brasil (BM). *A. F. Skutch* 4180, Costa Rica (BM). *Ynes Mexia* 4900, Brasil (BM).

Danaea simplicifolia Rudge
C. Appun s.n., Guyana (BM). *Giraud* Herb. Sag. 729, French Guyana (BM). *A. Hombersley* 69, Trinidad (BM). *P. W. Richards* 352, Guyana (BM). Ex herb. Rudge, French Guyana (BM).

Danaea sp. A.
A. H. G. Alston 7921, Colombia (BM). *P. J. Edwards and J. R. Woodhams* KER 1026, Guyana (BM + pteridophyte spirit collection B.72, K hort. 174–78.01484). *R. Persaud* 76, Guyana (K, NY, UG).

Marattia costulisora Alston
Clemens 5157, New Guinea (BM). *R. D. Hoogland and R. Pullen* 6091, New Guinea (BM). *C. Kalkman* 4909, New Guinea (BM).

Marattia fraxinea Smith
F. W. Andrews A1994, Sudan (BM). *H. Humbert* 8417, Zaire (BM). *R. W. J. Keay* FHI 28176, Nigeria (BM). *Newman and Whitmore* 475, Malawi (BM pteridophyte spirit collection T.8). *E. A. C. L. E. Schelpe* 3149, South Africa (BM). *E. A. C. L. E. Schelpe* 6241, Natal (BM). *M. E. Sofala* 2531A, Mocambique (BM). *Verdcourt* 62, Tanzania (BM).

Marattia laevis Smith
including *M. kaulfussii* J. Smith.
A. Cunningham s.n., Brasil, 1816 (BM). *R. A. and E. S. Howard* 8557, Dominica (BM). *E. P. Killip and A. C. Smith* 19145, Colombia (BM). *J. Miers* s.n., 1840, sine loco (BM). München Botanic Garden (BM + pteridophyte spirit collection S.273, K hort. 048–77.00205). *H. von Türkheim* 3058, Santo Domingo (BM).

Marattia rolandi-principis Rosenstock
Franc Rosenstock exsiccata 121, New Caledonia (BM).

Marattia werneri Rosenstock
including *M. coronata* Copel.
L. J. Brass 10765, New Guinea (BM). *L. J. Brass* 12116, New Guinea (BM). *R. D. Hoogland* 9258, New Guinea (BM). *Werner* 78, New Guinea (BM). *Werner* Rosenstock exsiccata 49, New Guinea (BM). *J. R. Woodhams* 127, New Guinea (BM + pteridophyte spirit collection S.281, K hort. 003–74.00116).

Macroglossum smithii (Racib.) Campbell
including *M. alidae* Copel.
A. H. G. Alston 13555, Hort. Bogor, Java (BM). *Boden Kloss* 19169, Sabah (BM). Hort. Bogor, II,K,(X)12, Java (K). *C. J. Brooks* 8277, Sumatra (BM). *C. J. Brooks* s.n., Sarawak (BM). *A. C. Jermy* 14223, Sarawak (BM + pteridophyte spirit collection W.368, W.392, K hort. 279–78.03064). *W. Meijer* 2294, Kalimantan (BM). *Orolfo* 9016, Sabah (BM). *M. Ramos* 1494, N. Borneo (BM). *H. S. Young* s.n., (Herb. Copeland 7), Sarawak (MICH). *H. S. Young* s.n., Sarawak (BM).

Angiopteris annamensis C. Chr. & Tard.
R. P. Cadière (F), Vietnam (BM). *R. P. Cadière* (G), Vietnam (BM). *J. and M. S. Clemens* 3725, Vietnam (BM). *Eberhardt* 1949, Vietnam (P).

Angiopteris elliptica Alderw.
A. H. G. Alston 15328, Sumatra (BM). *C. J. Brooks* 306.S, Sumatra (BM). *M. R. Henderson* 18774, Pahang (BM). *R. E. Holttum* s.n., Sarawak (BM + pteridophyte spirit collection S.274, K hort. 335–58.33504).

Angiopteris evecta (G. Forster) Hoffm.
P. J. Eyma 3745, Sulawesi (BM). *G. Forster* 438, Society Islands (BM). *A. Hecht* A, Cook Islands (K hort. 242–73.72306). *Hooker and Thompson* 351b, India (BM). *C. B. Kloss* s.n., Selangor (BM). *C. D. Sayers* 4, New Guinea (BM + pteridophyte spirit collection S.277, K hort. 723–63.72306). *Leeds University Expedition* P78, Ceylon (Leeds University Botanic Garden).

Angiopteris monstruosa Alderw.
C. J. Brooks s.n., Sumatra (BM).

Archangiopteris cadierei C. Chr. & Tard.
R. P. Cadière C, Vietnam (P).

Archangiopteris caudata Ching
specimens ex Herb. Kwangsi University, Southern Kwangsi, Oct. 2 1935 (PE).

Archangiopteris hokouensis Ching
Chu Ve-ming 1726, Yunnan (PE).

Archangiopteris itoi Shieh
C. M. Kuo 6698, Taiwan (BM).

Protomarattia tonkinensis Hayata
Cadière s.n., Vietnam, March–April 1934 (MICH, P). *Cadière* Fougère G, Vietnam, March 1934 (BM). *Cadière* Fougère G, Vietnam, March-April 1934 (P). *Cadière* Fougère G′, Vietnam, March–April 1934 (BM). *B. Hayata* s.n., Vietnam, 30 July 1917 (BM, P, TI). *B. Hayata* s.n., Vietnam, 8 August 1917 (M, TI). *Pételot* 3.956, Vietnam (BM).

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